A Comparative Study of the Wood Anatomy and Floral Vascular Systems of the New Zealand Genera of the Escalloniaceae, *Carpodetus*, *Ixerba* and *Quintinia*.

A thesis presented for the degree of Master of Science at the University of Canterbury, Christchurch, New Zealand

by P.V. Dravitzki

February, 1967.

LIST OF CONTENTS

INTRODUCTION

The New Zealand species of the Escalloniaceae are placed in three genera, Carpodetus, Ixerba and Quintinia (Allen, 1961). Some features which separate these genera are sufficiently striking to suggest that a comparison between them would be of interest. For example, the ovary is superior in Ixerba, half inferior in Carpodetus and sometimes fully inferior in Quintinia. Also, the phyllotaxis in most members of the family is spiral, whereas in Ixerba the leaves often stand opposite or in tightly aggregated verticils. Wood anatomy and the vascular system of the flower were selected for investigation, because they would provide two unrelated fields of new evidence. As each of these systems would provide a range of characters for comparison, it was expected that they would either confirm the grouping together of these genera within the ~~the~~ Escalloniaceae or that they might reveal important differences.

The genera which currently are grouped as the Escalloniaceae have been variously treated in past systems of classification. To cite some leading examples only, Bentham & Hooker (1867) treated them as a tribe (Escalloneae) of the Saxifragaceae within which they

also included genera now often segregated as the Grossulariaceae and Hydrangeaceae and other small families. Engler (1930) also included the Escalloneae as a tribe of the Saxifragaceae, but placed Ixerba with other genera in a separate tribe, the Brexeae. Hutchinson (1926, 1959) treats the Escalloniaceae as a separate family, and this opinion has been followed by many recent systematists. The principal reason underlying Hutchinson's recognition of the Escalloniaceae is his separation of the predominantly herbaceous Saxifragales from the almost exclusively woody Cunnoniales in which order the Escalloniaceae are placed.

In spite of these different treatments, it is evident that there has been no important disagreement over the usefulness of recognizing a group of genera centered round Escallonia. Opinions have differed on the less important problem of the hierarchical rank which should be assigned to this group. That is to say whether it should be given tribal or family rank.

The characters of the family are defined by Hutchinson (1959) as follows:

> Trees or shrubs; leaves simple, alternate, rarely subopposite or subverticillate, mostly with gland-tipped teeth; stipules absent; flowers ☿, rarely dioecious or polygamous, mostly racemose; sepals mostly united in the lower part, rarely free; imbricate or valvate, often persistent; petals free or rarely connate into a short tube, imbricate or valvate; stamens 5, rarely 4 or 6, sometimes alternating with

> staminodes, perigynous, free; anthers 2-locular, opening lengthwise; disk-lobes alternating with the stamens; ovary superior to quite inferior, syncarpous or rarely apocarpous, 1-6 locular; ovules numerous, parietal in the 1-locular ovaries, otherwise on central placentas; fruit a capsule or berry; seeds with small embryo and copious endosperm.

This definition does not contravene any of the features of the three New Zealand genera. However, the family is evidently based on a very general description and lacks any clearly defined diagnostic characteristics. Its members are woody plants with simple leaves, and the flowers are regular and actinomorphic with free petals an equal number of stamens and (usually) an inferior ovary comprising a variable number of carpels. Perhaps the characters most useful in unifying the group are the presence of a disc around the base of the style, and the small embryo with copious endosperm. It is this last character which distinguishes the Cunnoniales from the otherwise similar Rosales. Because of the general nature of the definition of the family it was considered desirable to examine fresh lines of evidence in the hope of adding further precision to the recognition of the group.

The genera of the Escalloniaceae are mostly confined to the southern hemisphere. The three genera dealt with here all have a restricted range. Ixerba is a monotypic genus endemic to the North Island of New Zealand and

Carpodetus is known from New Guinea and the Solomons and New Zealand (one endemic species). Quintinia occurs in the Phillipines, New Guinea, Australia, New Caledonia and New Zealand (3 endemic species).

CHAPTER II.

A COMPARISON OF THE VASCULAR SYSTEMS OF THE FLOWERS.

Methods.

Flowers of the three genera were examined by dissection under the binocular microscope, by clearing in lactic acid and in sodium hydroxide solution, and as serial microtome sections in the transverse and longitudinal planes. From this evidence detailed drawings of individual systems and schematic diagrams were built up.

CARPODETUS

The general morphology of the flower is represented in figs. 1 & 2. The ovary resembles an inverted cone and is crowned by five small sepals between which five triangular petals are inserted by broad bases. The summit of the ovary bears a prominent disc which is divided into five lobes by the bases of the filaments of the stamens which project between the lobes. The style is stout, erect and bears a prominent capitate stigma. The five loculi are mainly located in the lower part of the ovary, but project above the insertion of the whorls of the floral organs. The axile placenta in each loculus bears many ovules.

The vascular system of the flower of Carpodetus is represented by a series of transverse sections (fig. 3) (by drawing of a reconstruction of a portion of the bundles (fig. 4)) and by a simplified schematic

Fig. 1. Drawings of the flower of *Carpodetus serratus*

(A) Whole flower.

(B) Partly dissected flower.

(C) Petal.

(D) Stamen inner face.

(E) Stamen outer face.

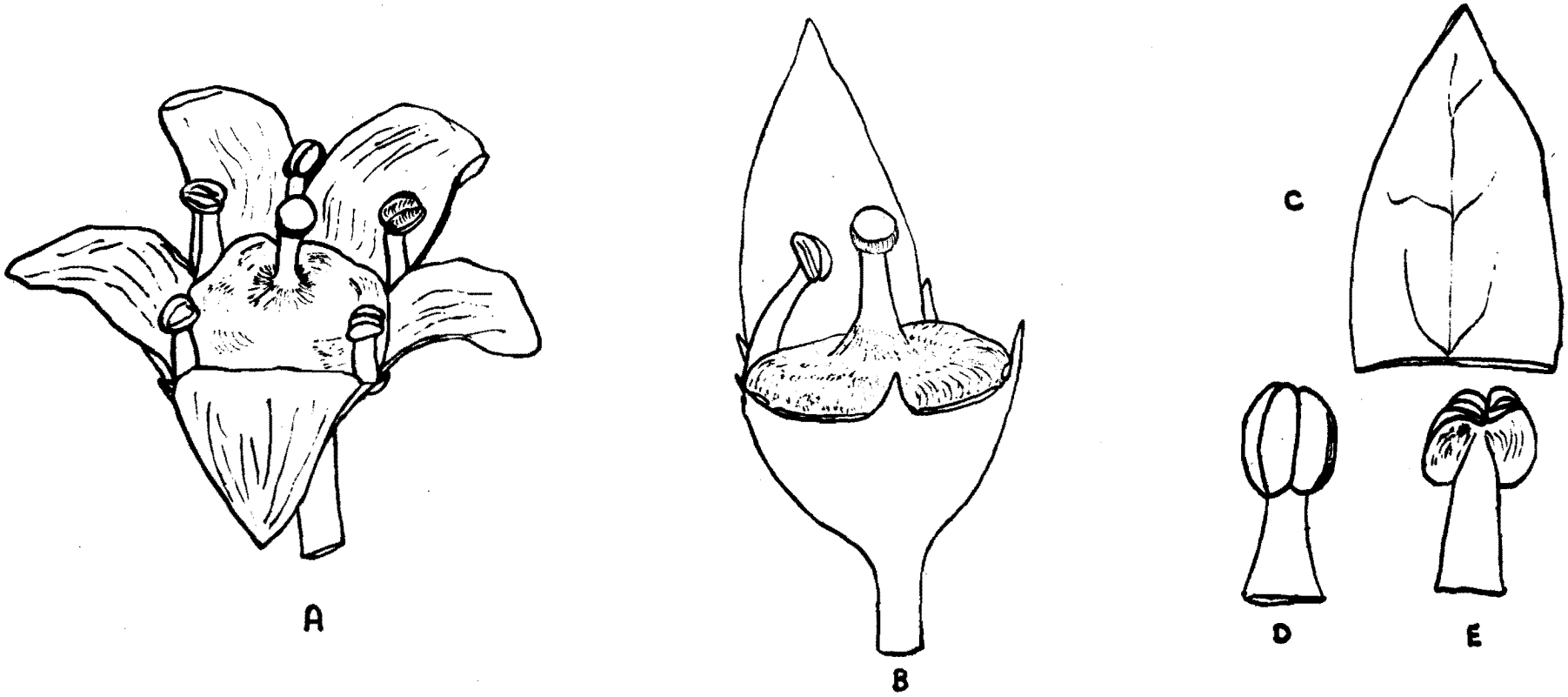
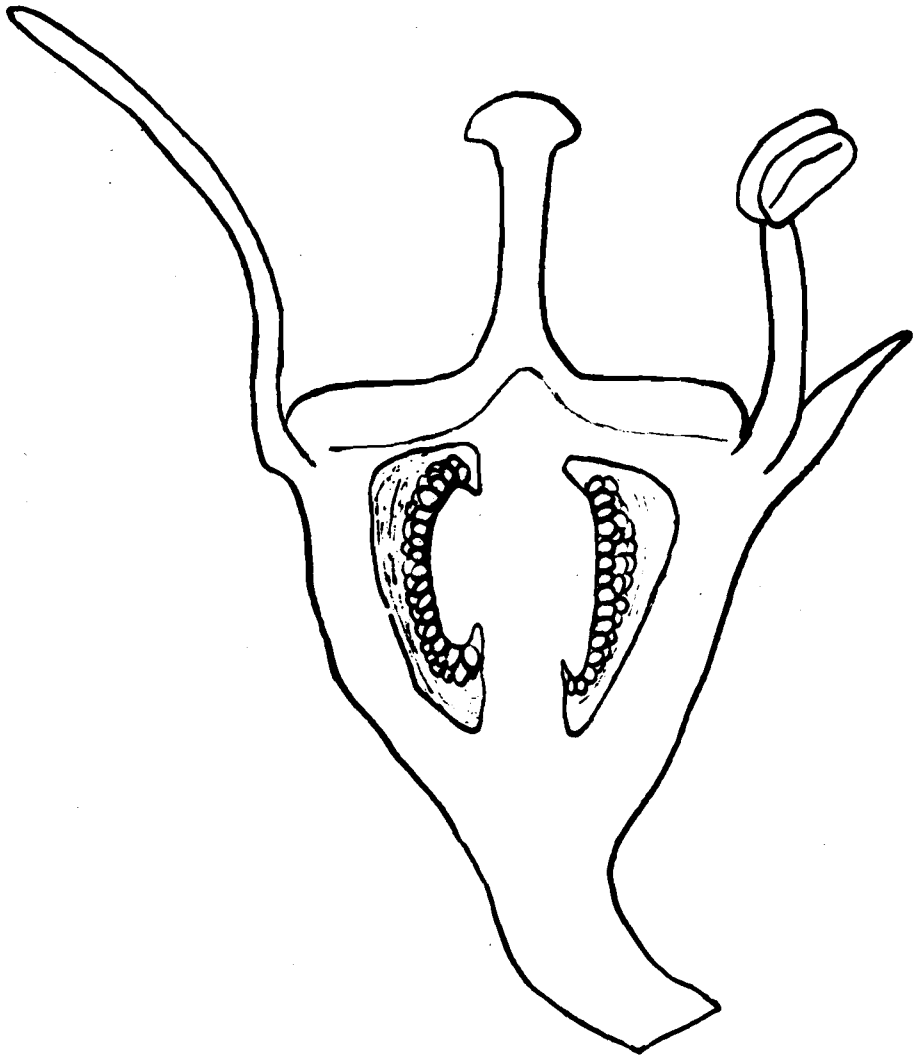


FIG. 1

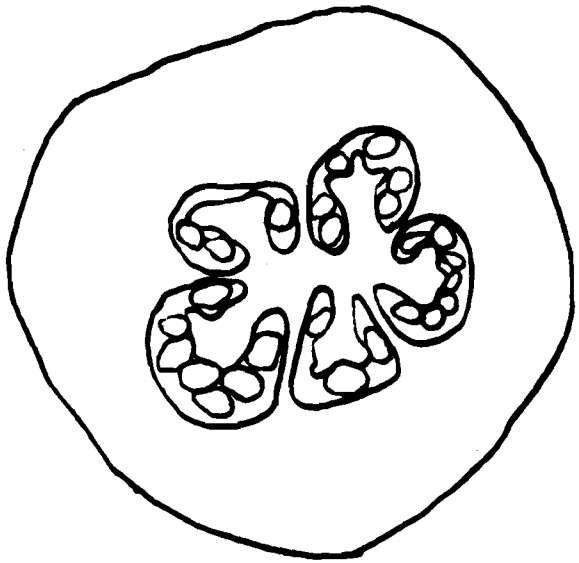
Fig. 2. Section views of Carpodetus serratus.

(A) Longitudinal section through the flower.

(B) Transverse section through the ovary.



A



B

FIG. 2

Fig. 3. Selected transverse sections through the ovary of *Carpodetus serratus*.

(A) Section through the lower part of the ovar

Three ventral traces can be clearly seen; two of the bundles in the outer framework have not yet diverged into separate petal and stamen traces.

(B) Section through the ovary at a point approximately half-way up.

Alternating petal and stamen-sepal bundles seen around the edge and closer to the loculi are the dorsal and disc bundles which have branched from the outer framework.

(C) Section through the top of the ovary and d

Sepals, stamens and petals now separate. Many of the disc bundles have faded out leaving mainly the dorsals and ventrals which will continue into the style.

(d = dorsal; v = ventral; p = petal trac

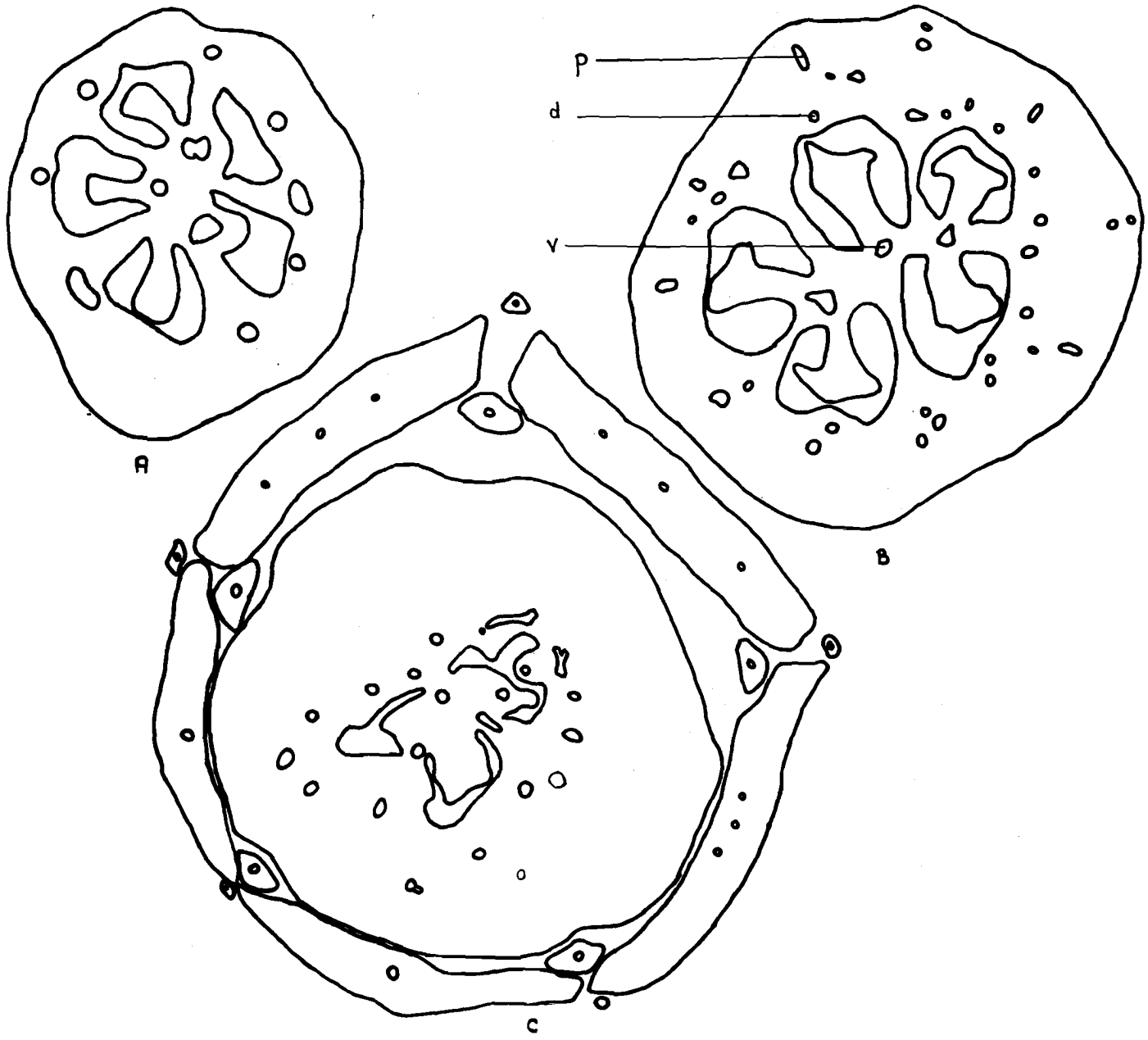


FIG 3

Fig. 4. A reconstruction of a portion of the bundles in the flower of Carpodetus serratus.

Dorsal arises from petal trace near base of ovary. At the top of the ovary it unites with the ventrals and some of the inner disc traces and continues into the style. Stamen and sepal traces diverge from the one trace and arising from them are other disc traces.

(d = dorsal; v = ventral).

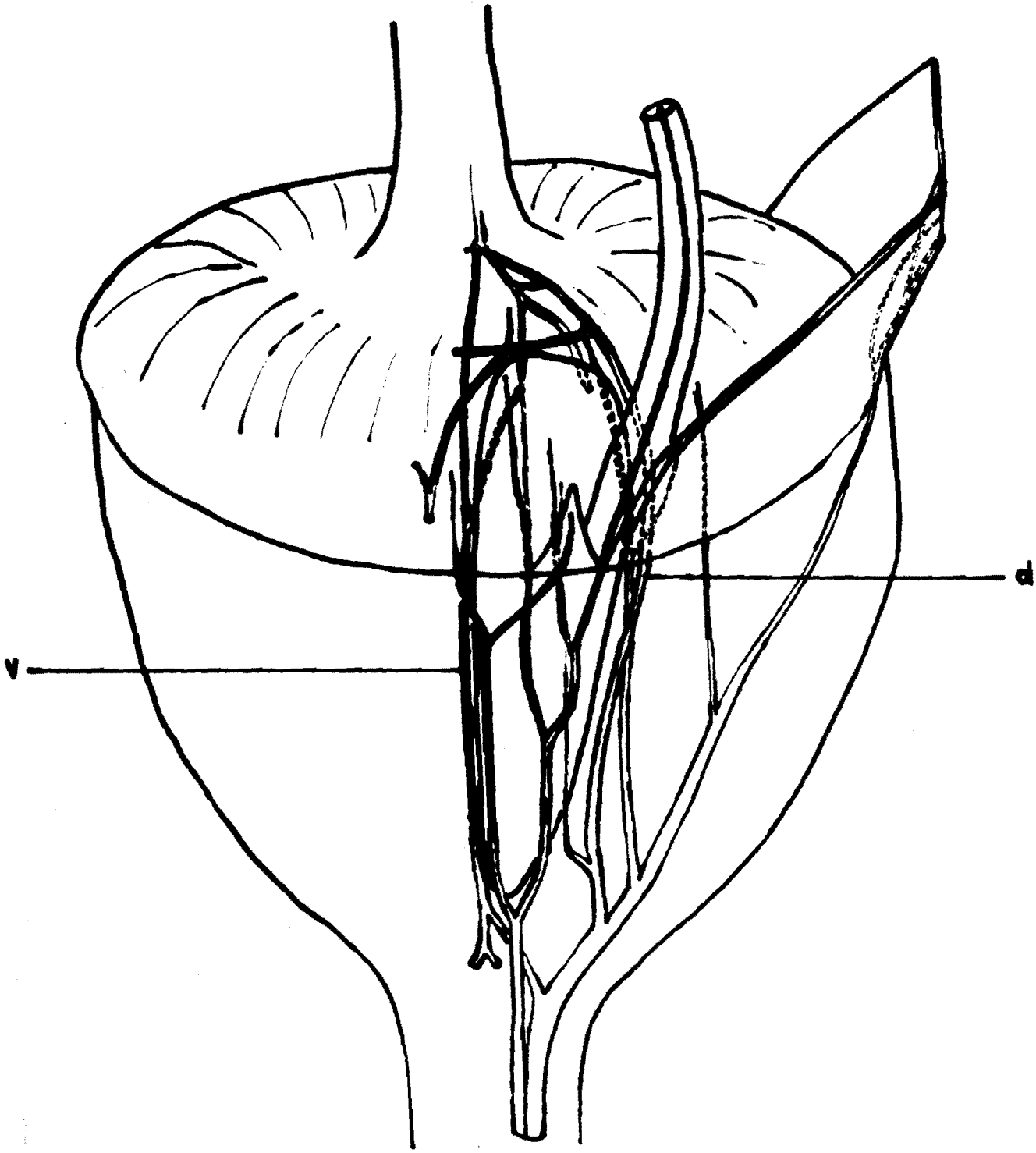
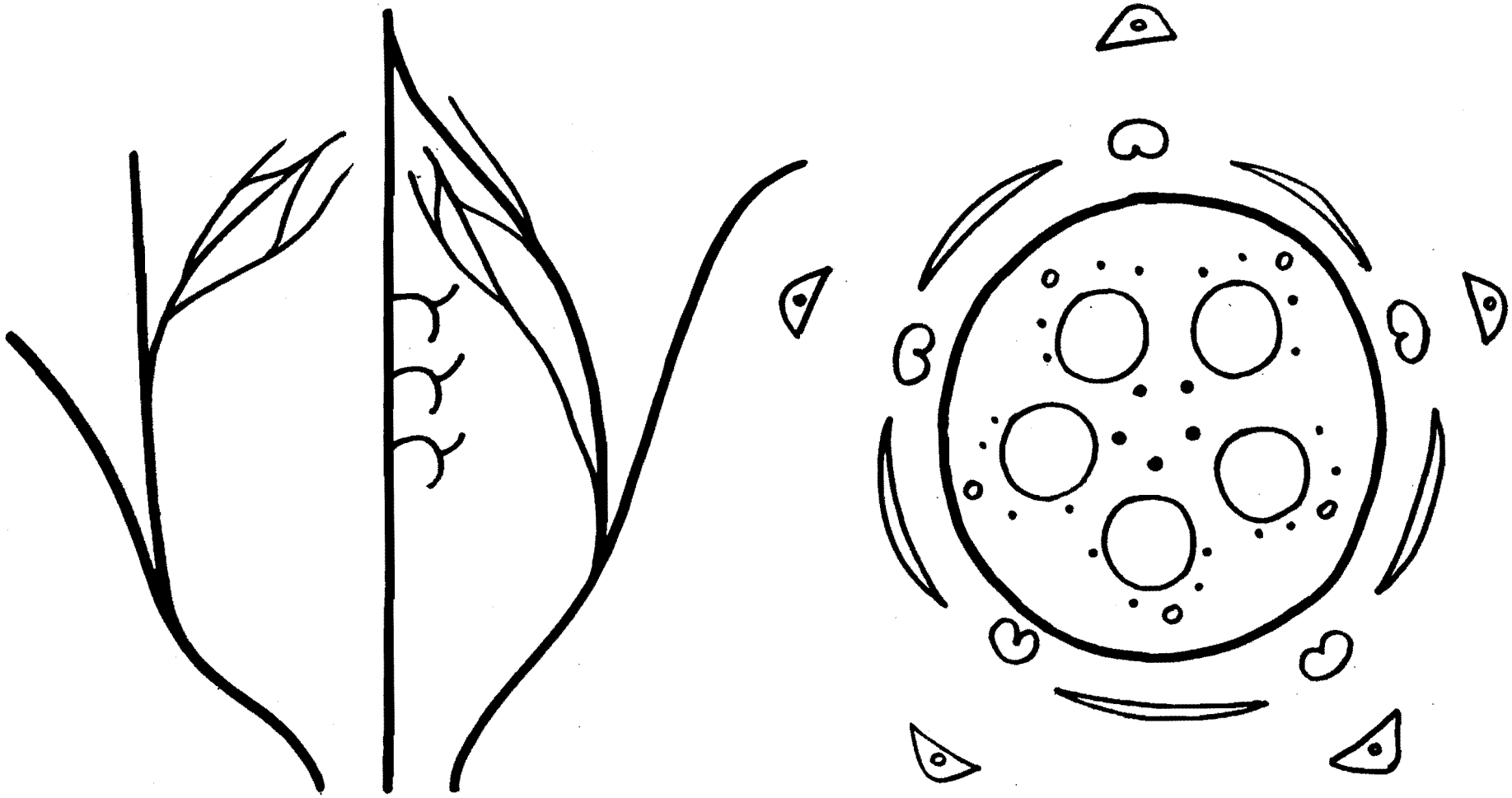


FIG. 4

Fig. 5. Simplified schematic reconstruction of vascular system of Carpodetus serratus

(A) Longitudinal view

(B) Transverse view



A

FIG. 5

B

reconstruction (fig. 5). The whole vasculature can be visualised as three systems of bundles. The first is an outer framework of bundles which diverge from the pedicel in the outer wall of the ovary: of these, five supply the sepals and stamens, and five the petals. These bundles unite in an asymmetrical and variable manner as they approach the pedicel. In their upper course they give off branches to the inner side. These form the second vascular system of which the bundles either end blindly in the disc (after linking with other similar bundles to form a reticulum) or five of them continue upwards as the vascular supply of the styles. These are the dorsal bundles of the five carpels. The third system comprises the ventral bundles of the carpels. These are not entirely regular, but may be represented (as in fig. 5B) as one bundle opposite each placenta. From these axial ventrals numerous ovular bundles are given off. The ventrals continue upwards to meet the dorsals in the style.

IXERBA

The comparatively large flowers of Ixerba are characterized by a clearly superior ovary with a long tapering and characteristically bent style (figs. 6 & 7). There is no prominent stigmatic swelling. Around the base of the ovary is a disc with five prominent lobes. The long staminal filaments project between the lobes of the disc, and bear

Fig. 6. Drawings of the flower of Ixerba brexioides

(A) Whole flower

(B) Flower with the sepals, petals and stamens removed

(C) Petal

(D) Small sepal

(E) Large sepal

(F) Stamen inner face

(G) Stamen outer face

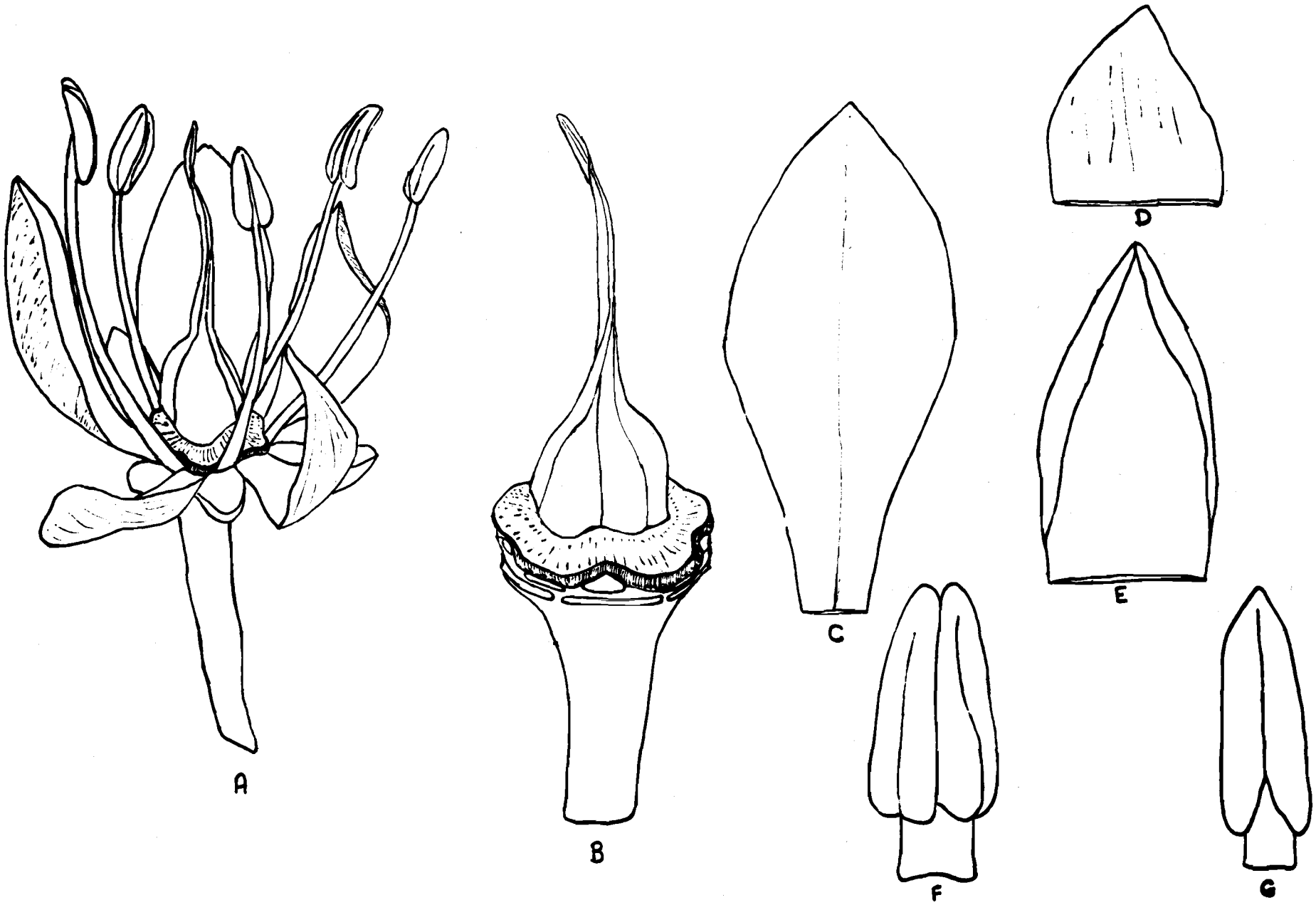
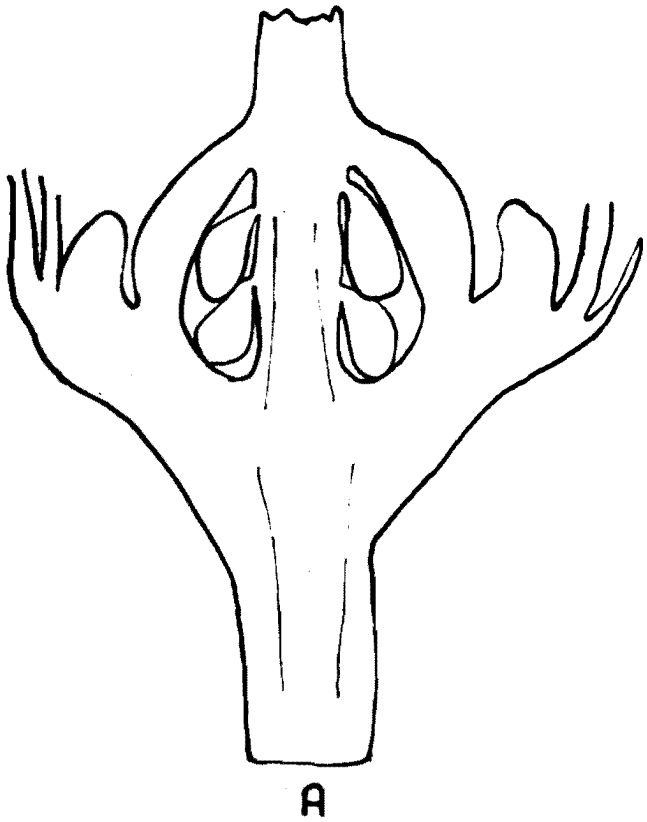


FIG. 6

Fig. 7. Section views of the flower of Ixerba brexioides

(A) Longitudinal section

(B) Transverse section at mid-ovary level



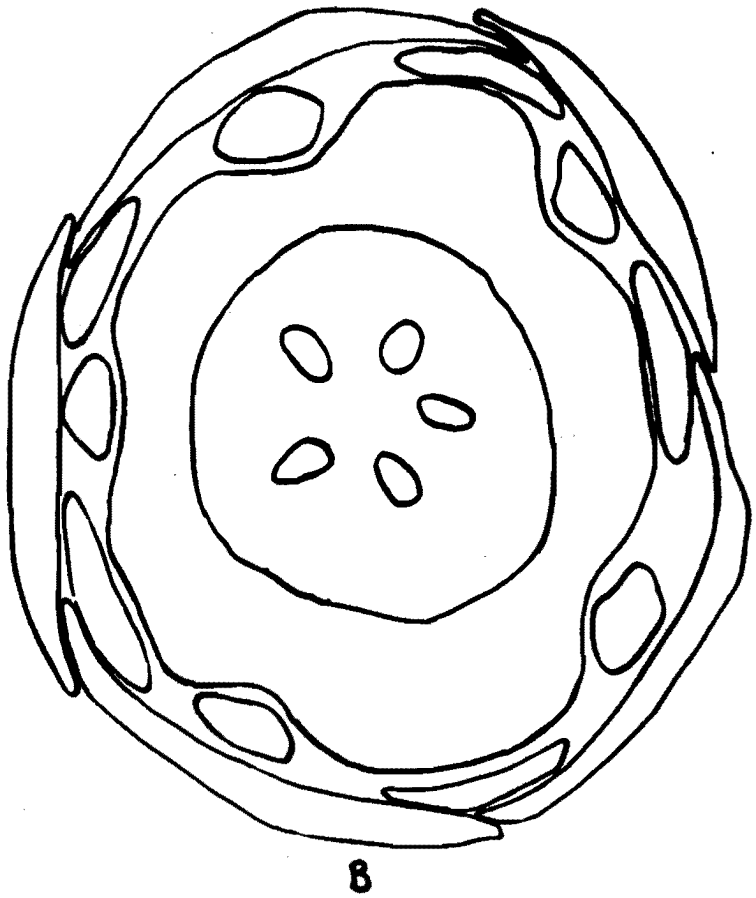


FIG. 7

small anthers. The petals are inserted by a comparatively narrow base and alternate with five fleshy and broadly based sepals. The five loculi each contain two ovules lying side by side and one slightly above the other. The vascular system of Ixerba closely resembles that of Carpodetus. The same three systems of bundles can be seen. (figs. 8, 9 & 10). Differences in the first two systems are that the staminal and sepal bundles diverge in the pedicel, not in the ovary wall and that the dorsal bundles also arise at a lower level. Both these differences are related to the superior position of the ovary. The supply of bundles ending in the disc is more abundant than in Carpodetus as the stamen bundles, petal bundles and dorsal bundles all give off branches which end in the disc. The dorsal is difficult to identify as besides giving off several small traces to the outside which end blindly in the disc it also produces to the inside a number of fine bundles which continue up through the ovary wall. A further difference seen in the outermost system is that the sepal is supplied laterally by a branch of the adjacent petal bundle. This branch is indicated in fig. 9 but is not drawn in fully in an attempt to keep the diagram as clear as possible. The third (ventral) system is also slightly modified in comparison with Carpodetus. In the lower part of the ovary the ventral system forms a cylinder or close ring of bundles which runs up to the central axial core. Ovular bundles are given off to the two ovules in

Fig. 8. Selected transverse sections through the flower of Ixerba brexioides.

(A) Section through the receptacle.

Ventrals have branched from the outer framework; stamens and sepal traces clearly separate in three bundles already.

(B) Section through the base of the ovary (beginnings of two loculi shown)

Ventrals unite more or less into a cylinder. All stamen and sepal traces have separated from their common bundles as have the dorsal bundles from the petal traces. Disc bundles have branched out from most of the stamen and petal traces.

(C) Section through the flower at the level of the base of the stamens. (N.B. this flower has six loculi and flower parts are in sixes instead of the usual fives)

A profuse development of small bundles shown. These can be largely grouped into an outer ring which end in the disc and an inner ring which run up the ovary wall. The dorsal is difficult to identify from among all these bundles. The lateral traces in the sepal which have arisen from the petal trace are clearly seen.

(v = ventral; d = dorsal; p = petal trac

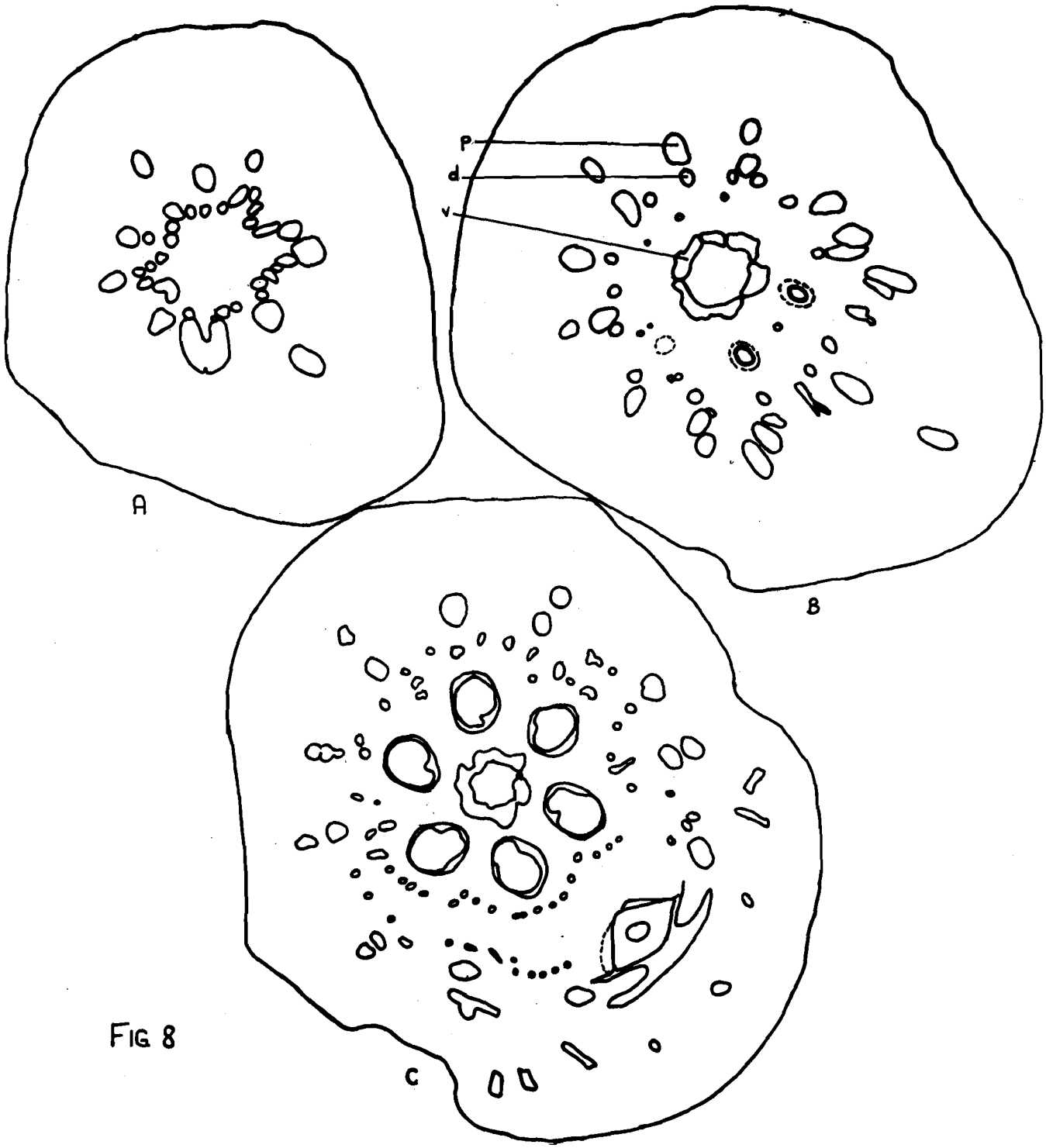


FIG 8

Fig. 9. A reconstruction of a portion of the vascular system of the flower of Ixerba brexioides.

Stamen and sepal traces separate low down in the receptacle. Branches arise from the stamen trace, petal trace and dorsal which either end in the disc or continue into the ovary wall. Dorsal difficult to distinguish but it continues up into the style while most bundles in the ovary wall gradually fade out.

(v = ventral; d = dorsal; p = petal trace; s = trace which branches into several lateral traces of the sepal.)

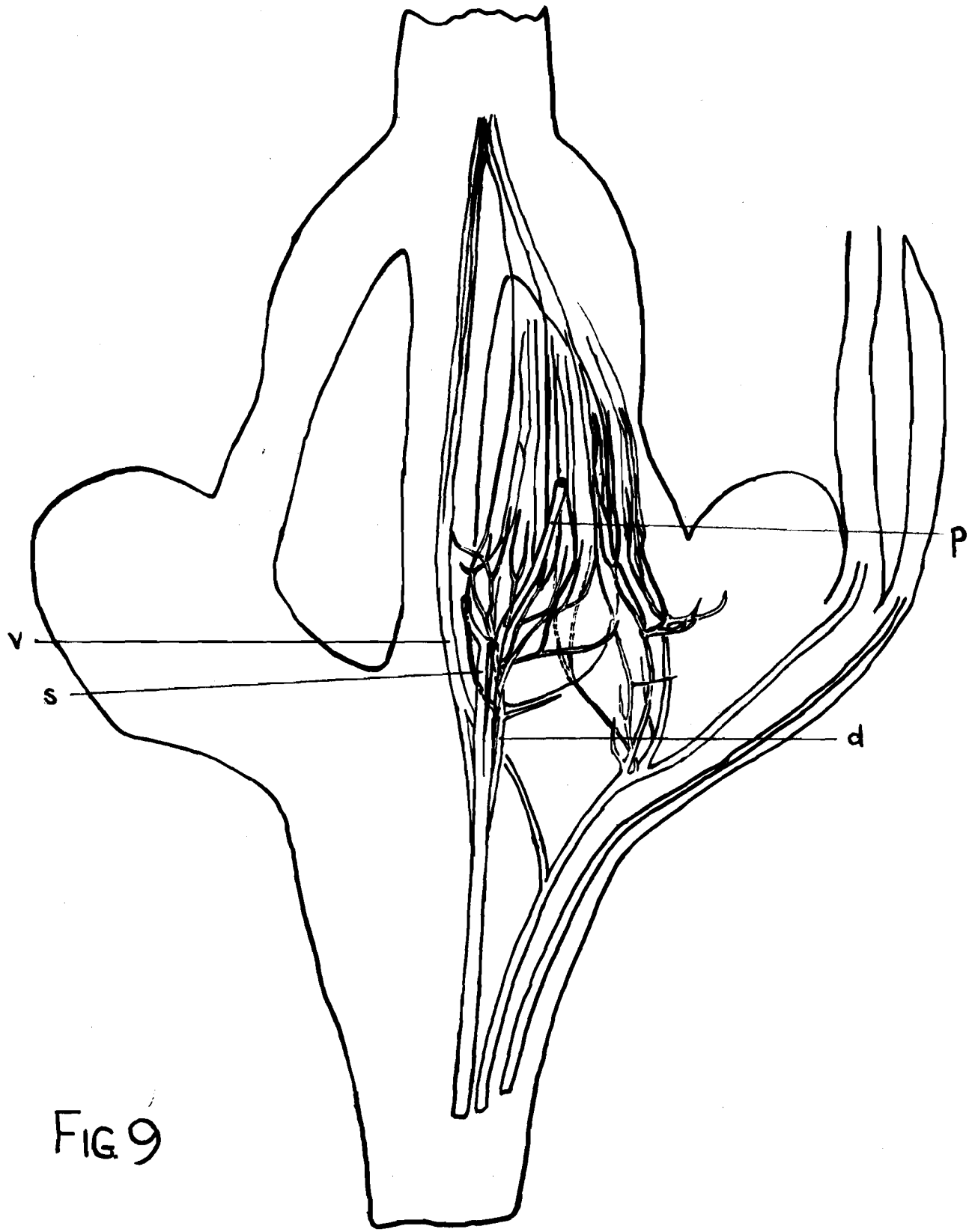


FIG 9

Fig. 10. Simplified schematic reconstruction of the vascular system of the flower of Ixerba brexioides

(A) Longitudinal section

(B) Transverse section at mid-ovary level.

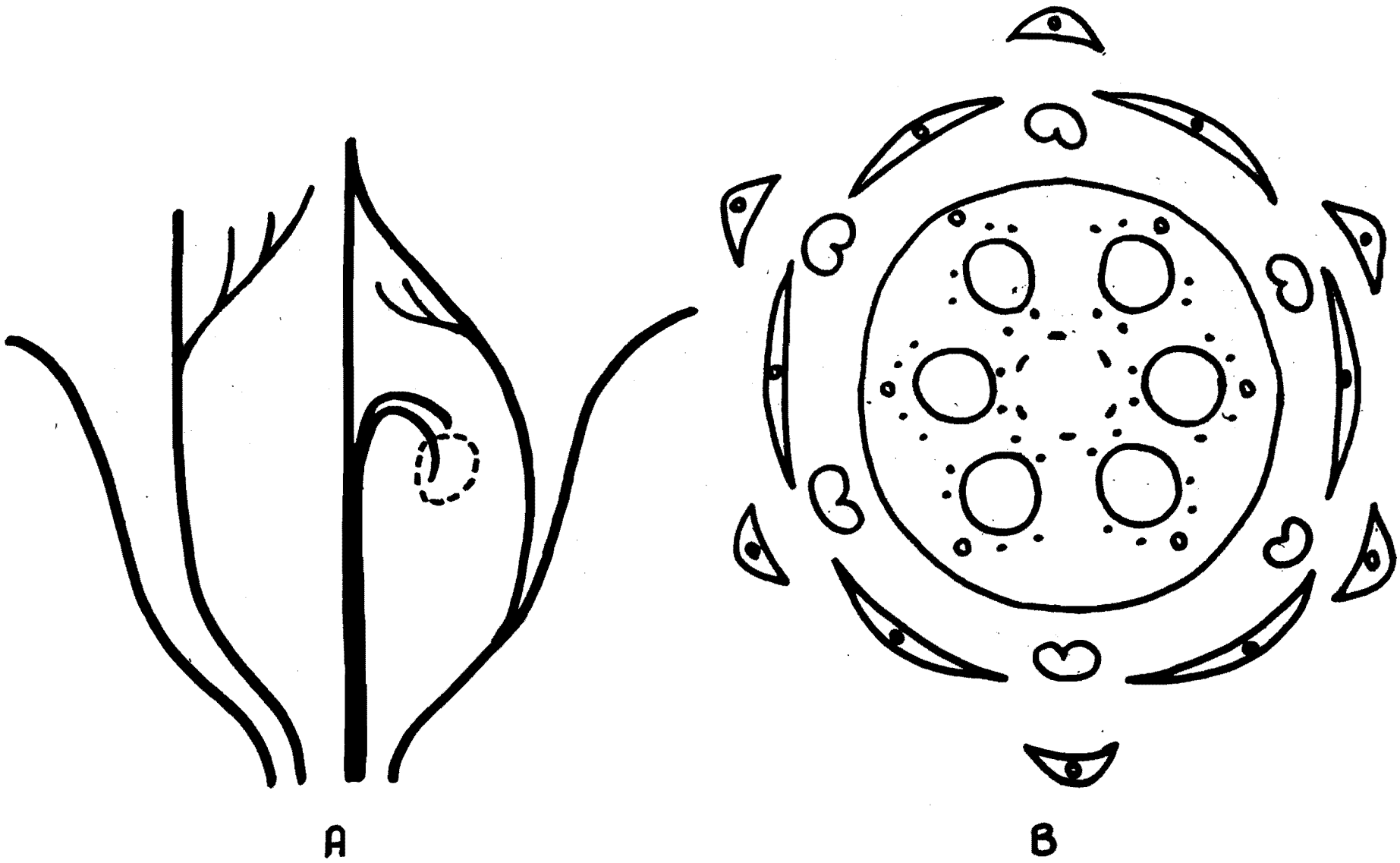


FIG. 10

each loculus. The system continues upwards by bundles lying in the planes between the carpels and these meet the dorsals in the style.

QUINTINIA

The morphology of the flower of Quintinia is similar to that of Carpodetus. Figs. 11 & 12 are drawn from Q.acutifolia. The principal external difference between the two flowers is the shape of the petals - spathulate with narrow base in Quintinia, triangular and broad based in Carpodetus. The ovary differs in bearing generally fewer carpels (loculi) than there are stamens. There are several ovules in each loculus.

As can be seen from figs. 13, 14 & 15 the vascular system of the flower is basically similar to that of the genera previously described. However, the difference in number between the carpels and the outer floral whorls leads to a less symmetrical linking between the dorsal system and the outer framework of bundles. (In fig. 14 the dorsal shown arises from the petal trace but in this flower the other two dorsal bundles arise from the stamen-sepal trace). The ventral system consists of two bundles running up the axis adjacent to each placenta (that is, six bundles in the typically three-carpellate flower). Ovular bundles are given off by each of these ventrals before they continue into the style to meet the dorsals.

Fig. 11. Drawings of flower of Quintinia acutifolia

(A) Whole flower

(B) Flower with sepals, petals and stamens removed

(C) Petal

(D) Stamen inner face

(E) Stamen outer face

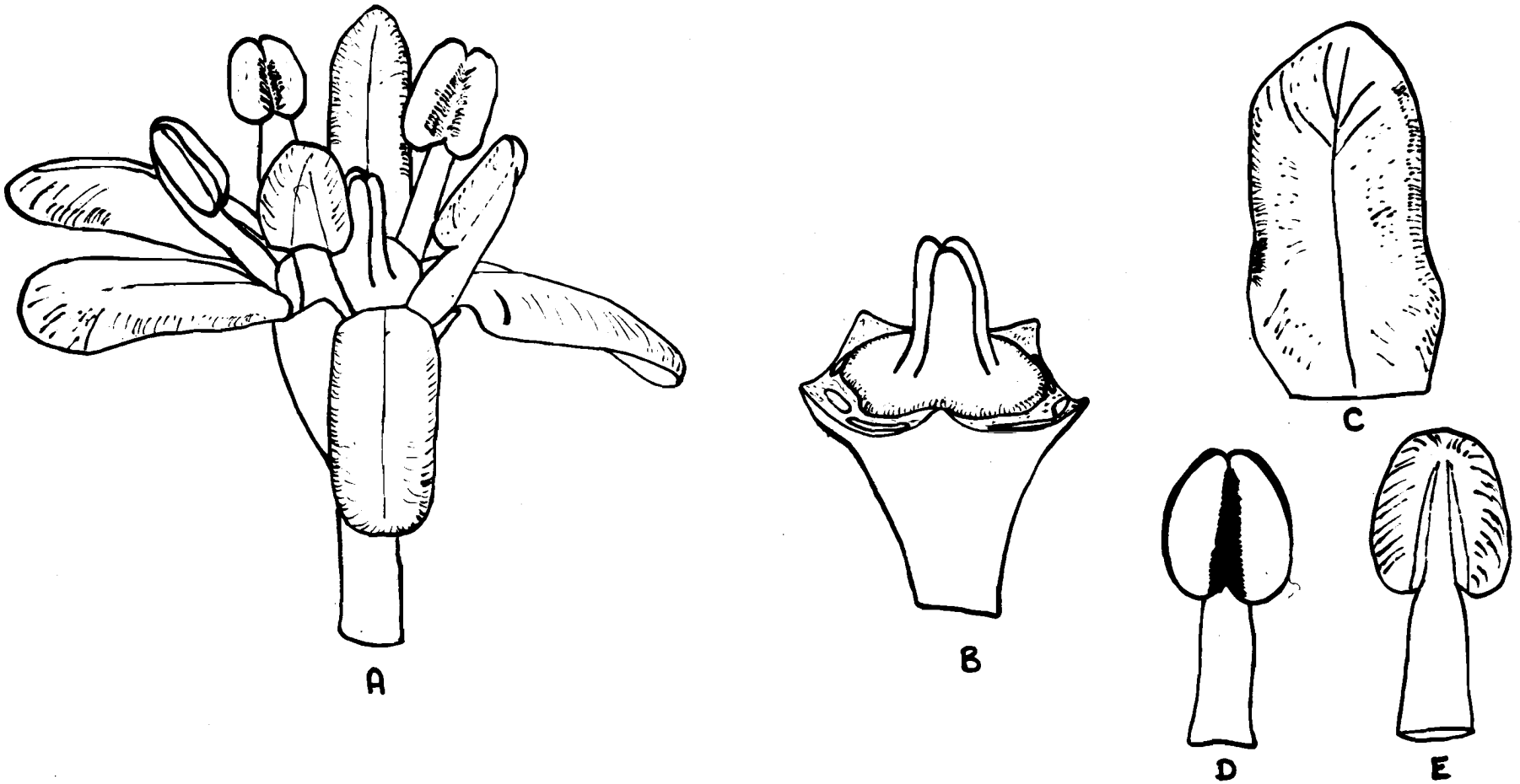
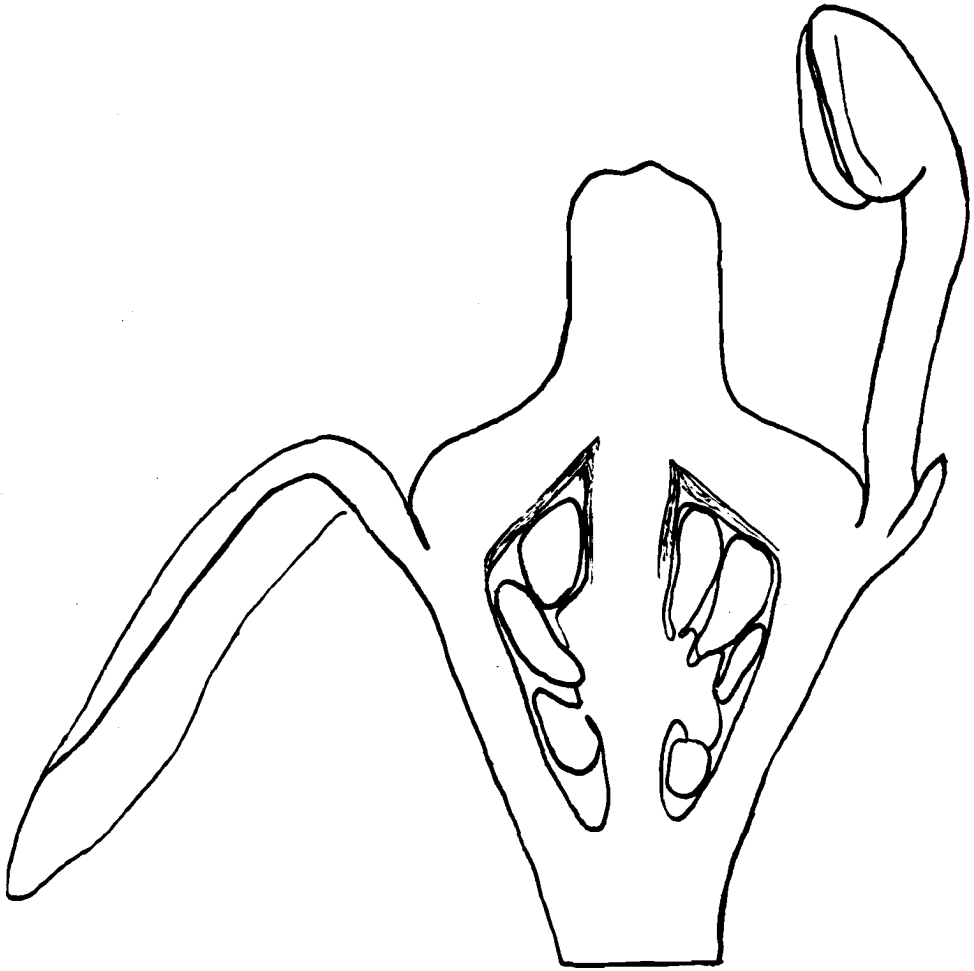


FIG. 11

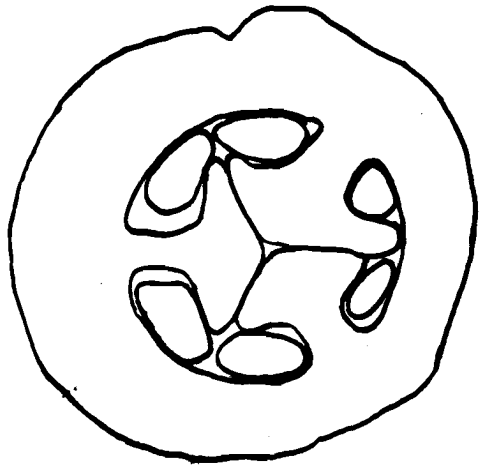
Fig. 12. Section view of flower of Quintinia acutifolia

(A) Longitudinal section

(B) Transverse section at mid-ovary level



A



B

FIG. 12

Fig. 13. Selected transverse sections through the flower of Quintinia acutifolia

(A) Section through the ovary at a low level.

Ventrals have separated off well before. The ten bundles of the outer framework (five petals and 5 stamen sepals) clearly visible.

(B) Section through ovary less than half way up.

Dorsals seen to have branched off; one has arisen from a petal trace and the other two from stamen-sepal traces.

(C) Section through ovary a little above the half way level.

Dorsals clearly separate; most of the stamen end sepal traces have separated.

(D) Section through the flower at the top of the ovary level.

A ring of small disc bundles shown. These have arisen from petal traces, the dorsal and the stamen sepal traces.

(E) Section through flower above the ovary.

Flower parts separate; dorsals clearly visible near the very reduced loculi.

(v = ventral; d = dorsal; p = petal trace

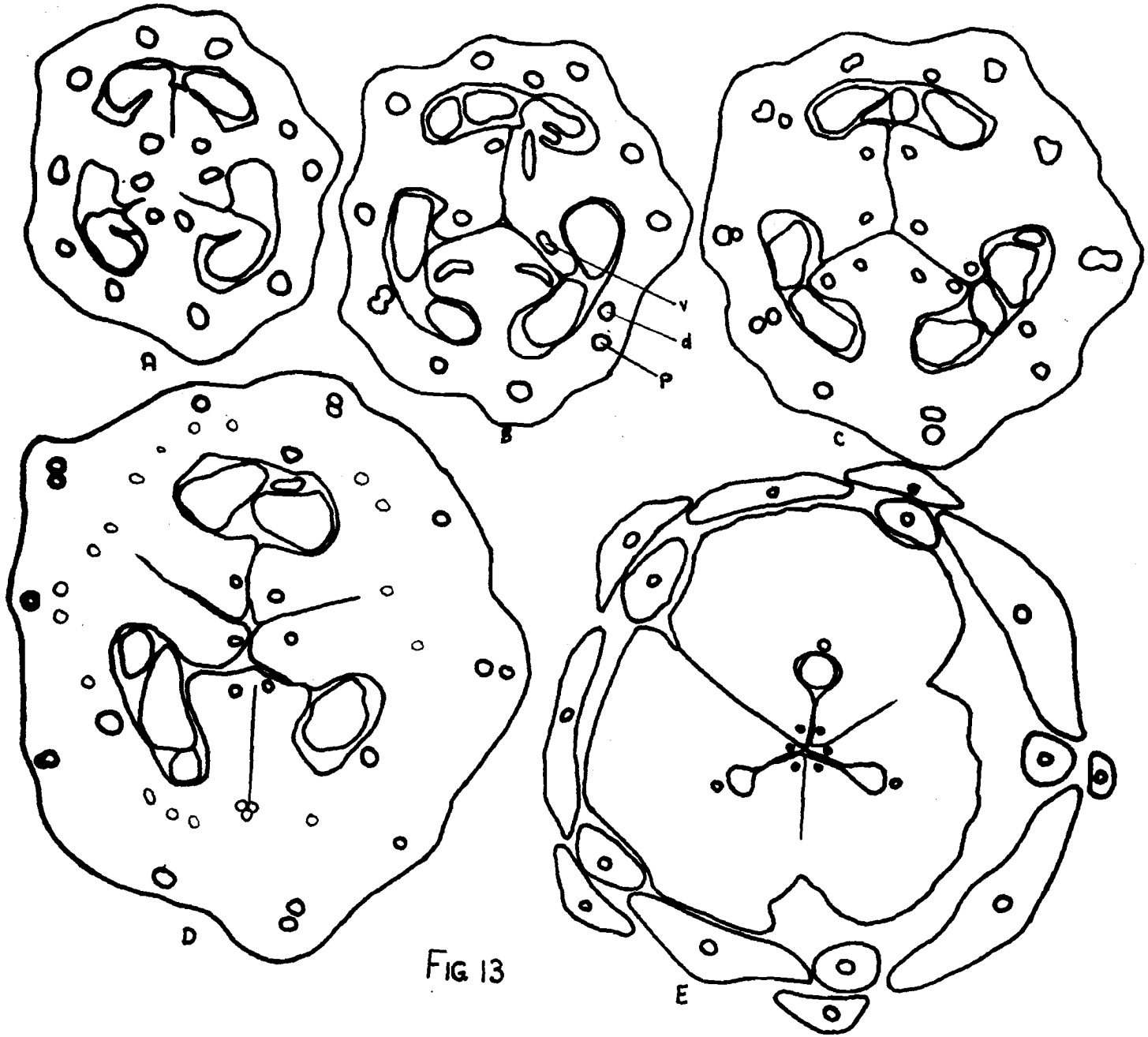


FIG 13

Fig. 14. A reconstruction of a portion of the vascular system of the flower of Quintinia acutifolia

Dorsal runs up into the style and fuses with the ventral system. Limited number of bundles which end blindly in the disc.

(d = dorsal; v = ventral; p = petal trace)

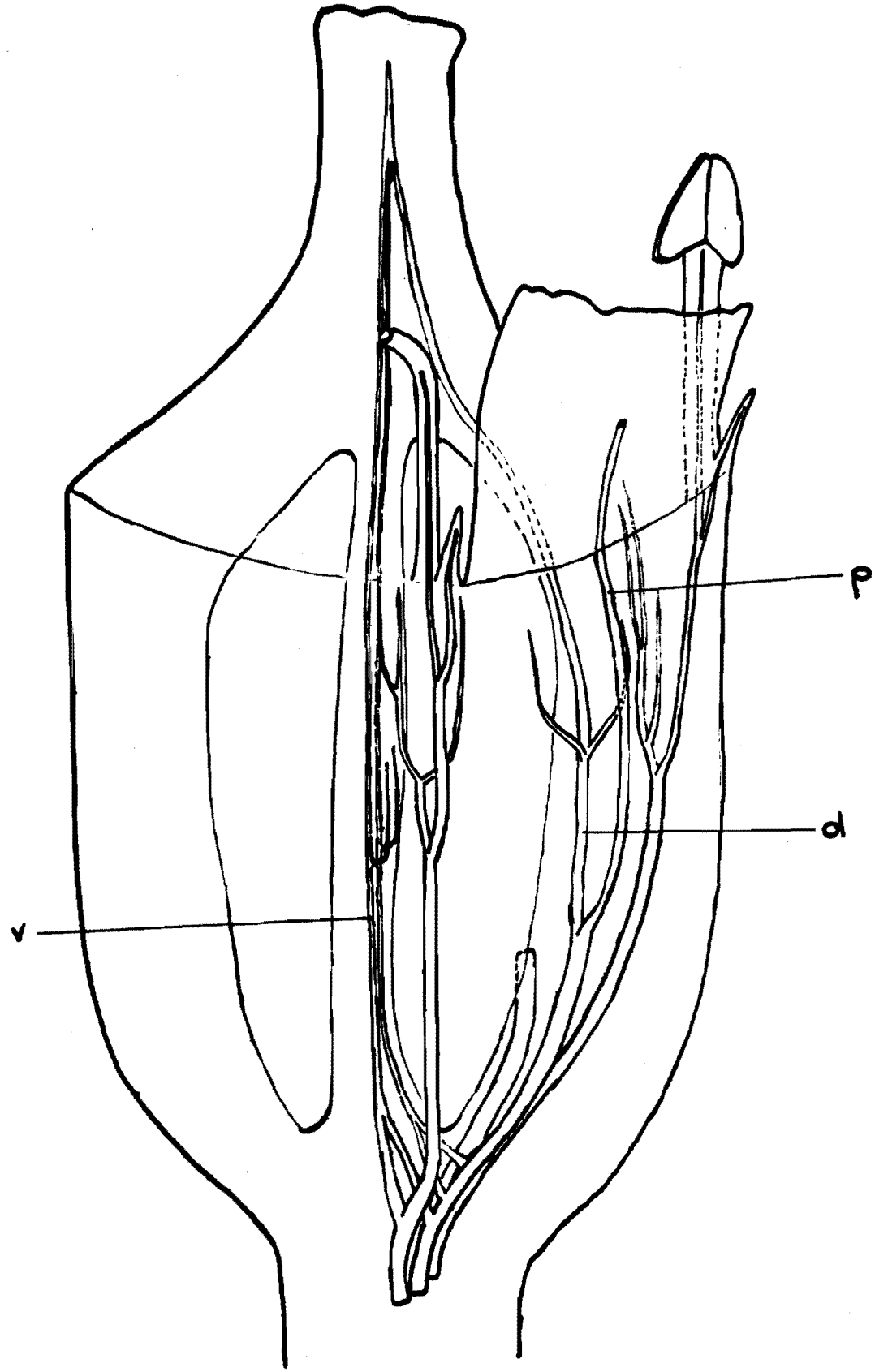


FIG 14

Fig. 15. Simplified schematic reconstruction of vascular system of Quintinia acutifolia.

(A) Longitudinal section

(B) Transverse section.

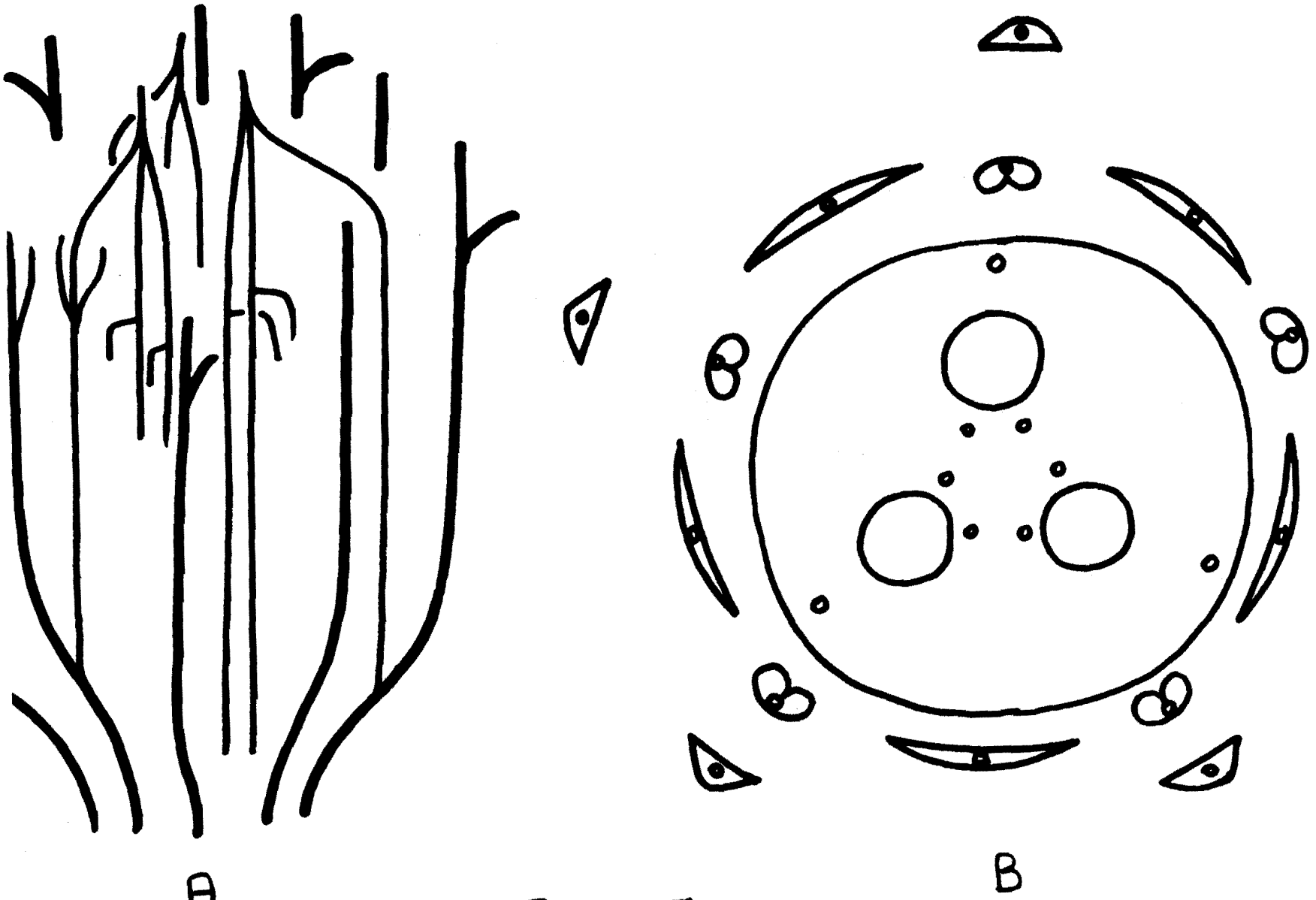


FIG. 15

ESCALLONIA

For the sake of comparison the morphology of the Escallonia, the type genus of the family, was investigated. The flower of E. exoniensis (figs. 16 & 17) has a half-inferior ovary and a short floral tube on which are borne the sepals, petals and stamens. The lower portion of the ovary is divided into two loculi, but higher up the placentas become free and parietal on the sides of a single loculus.
The vascular supply as shown in figs. 18, 19 & 20 includes an outer system which diverges from the ovary wall into the floral tube: it comprises the supply to the sepals, petals and stamens. Prominent in this outer system in the ovary wall are several bundles which end blindly at the point where the floral tube joins with the ovary wall. These bundles are thought to supply nectaries in this position. From the outer system the second system branches towards the centre of the flower where it forms a closely branched disc-supply and continues upwards as the dorsals and subsidiary style-bundles. The ventral system consists of two bundles (one in each placenta) each of which divides in its upper course to give branches which unite with the dorsal supply to the style.

CONCLUSIONS

The flowers of these three New Zealand genera are all regular and simple, with few distinctive features. Differences between them mainly concern the number of

Fig. 16. Drawings of flower of Escallonia exoniensis

(A) Whole flower

(B) Longitudinal section view of flower

(C) Petal

(D) Stamen inner face

(E) Stamen outer face

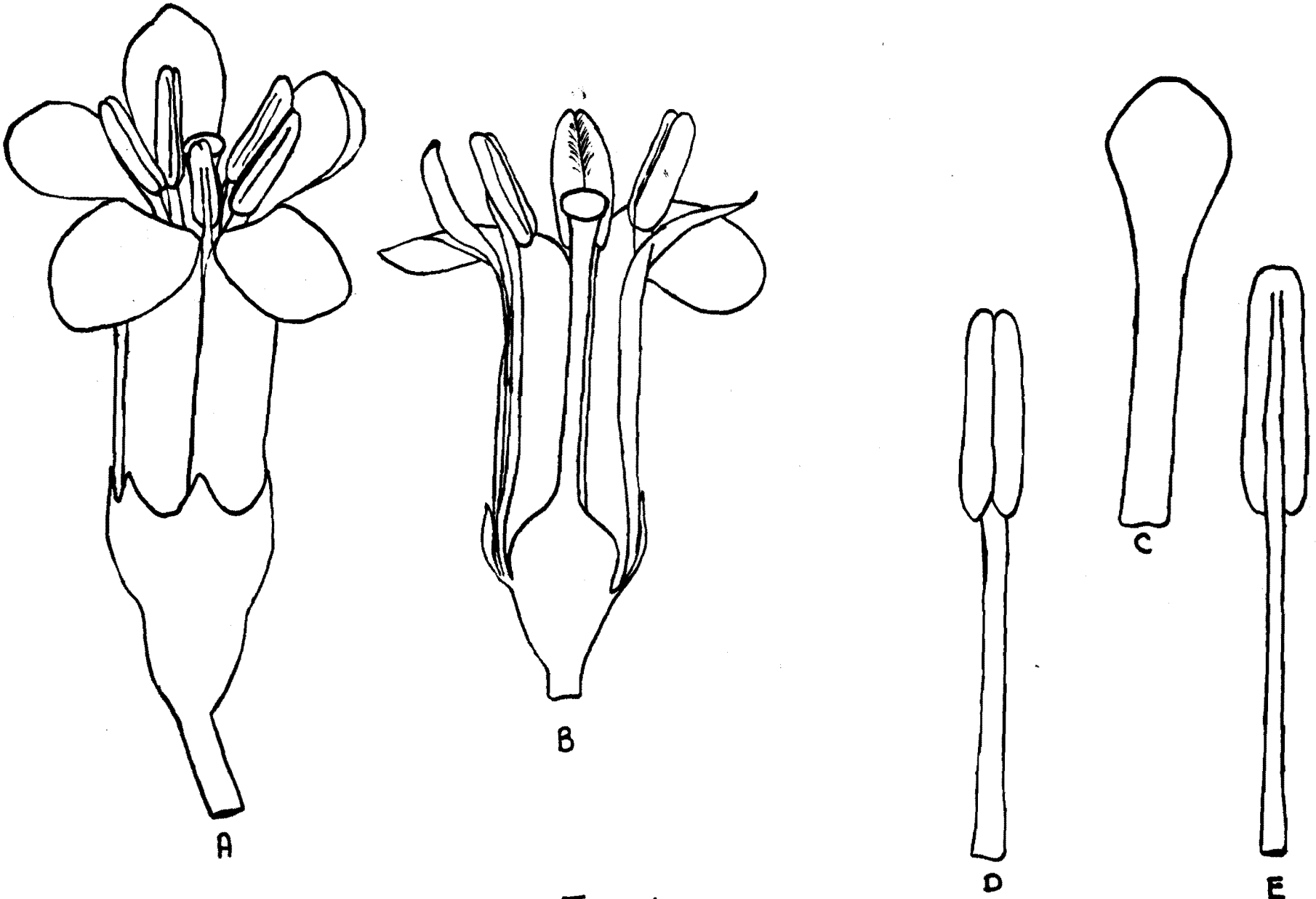


FIG. 16

Fig. 17. Section views of flower of *Escallonia exoniensis*

(A & B) Longitudinal sections in planes at right angles to each other.

(C) Transverse section at mid-ovary level

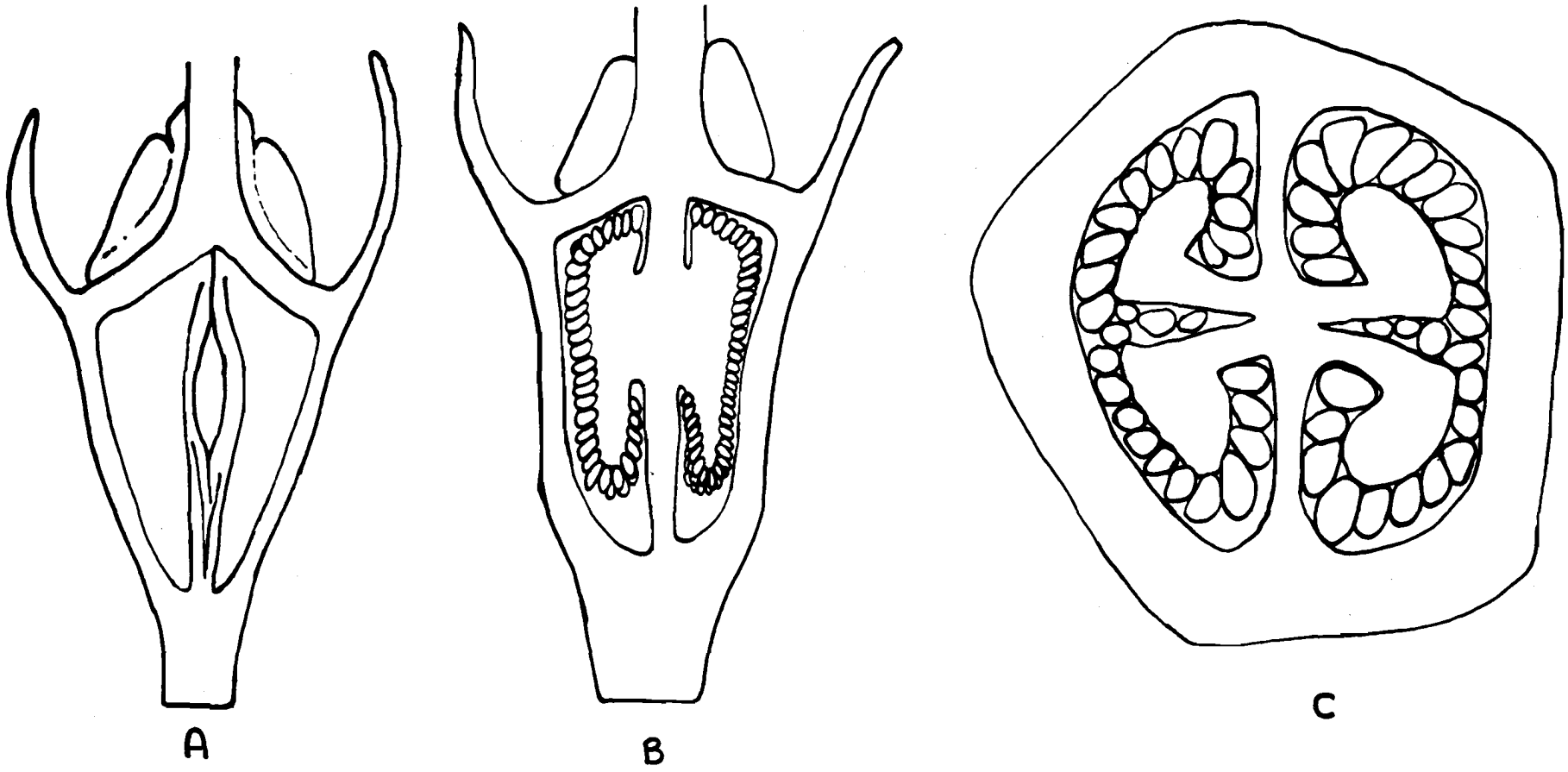


FIG. 17

Fig. 18. Selected transverse sections through the flower of Escallonia exoniensis.

(A) Section through the flower at a low level.

Ovary divided into two loculi. In the outer wall are the bundles of the outer vascular framework; the two ventrals can be seen in the portion between the loculi.

(B) Section through the ovary at a mid ovary level.

Placentae have become free and parietal, forming a single loculus in the ovary.

(C) Section through the flower at an upper ovary level.

Inner framework of interlacing bundles branching off from the outer framework.

(D) Section through the flower at the top of the ovary.

Prominent nectary traces in ovary wall fading or faded out. Inner network of small bundles continue upwards towards style.

(E) Section through flower above the ovary.

Outer vascular framework in the floral tube. Inner framework continues upwards, most of the bundles gradually fading out. Ventral bundles have divided.

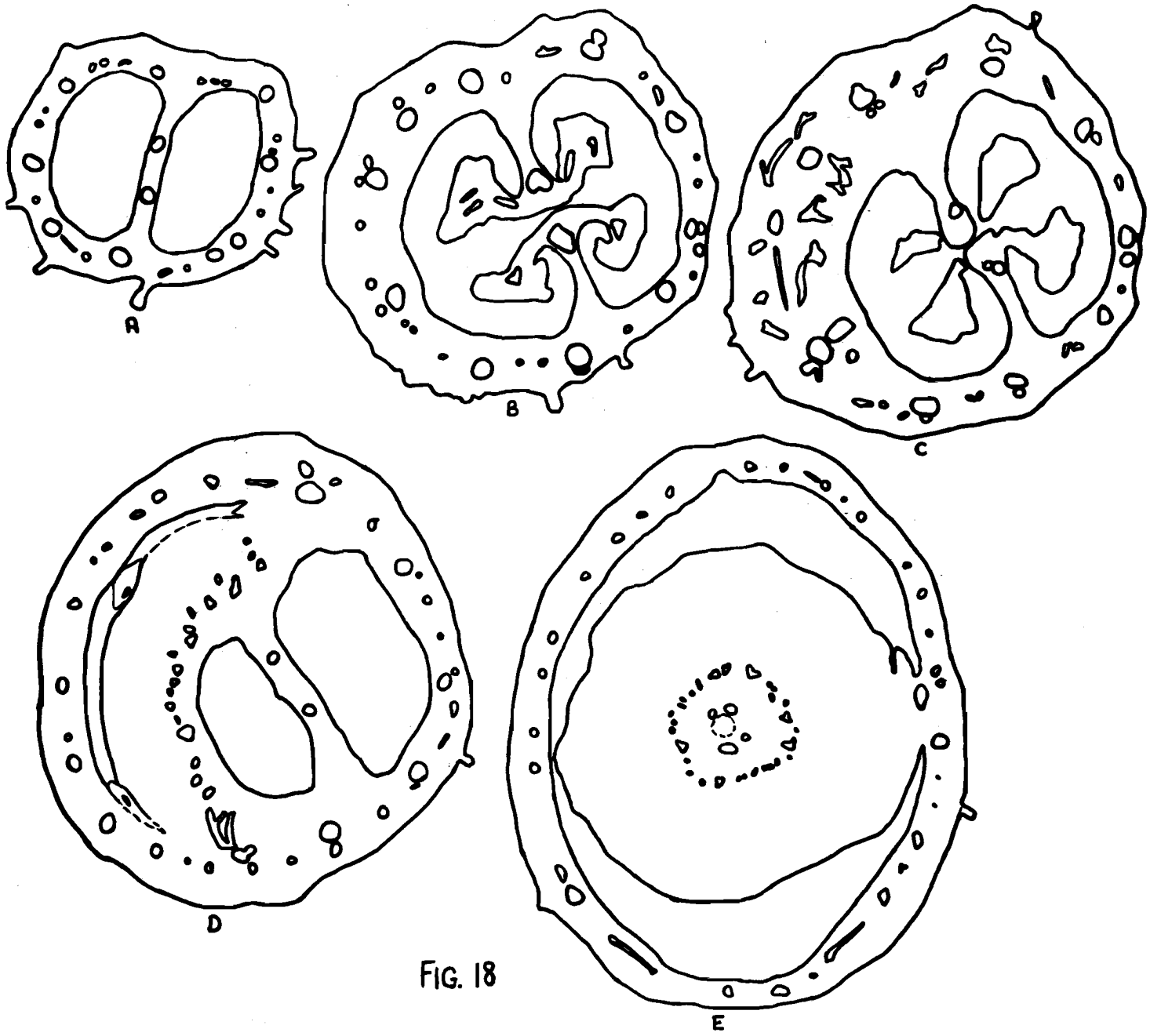


FIG. 18

Fig. 19. A reconstruction of a portion of the vascular system of the flower of Escallonia exoniensis

Outer framework of vessels continues up into floral tube; nectary bundles prominent in ovary wall and at the base of the floral tube. A few of the largest bundles of the inner network continue up into the style and fuse with the branches of the ventrals. These bundles presumably represent the dorsals.

(v = ventral)

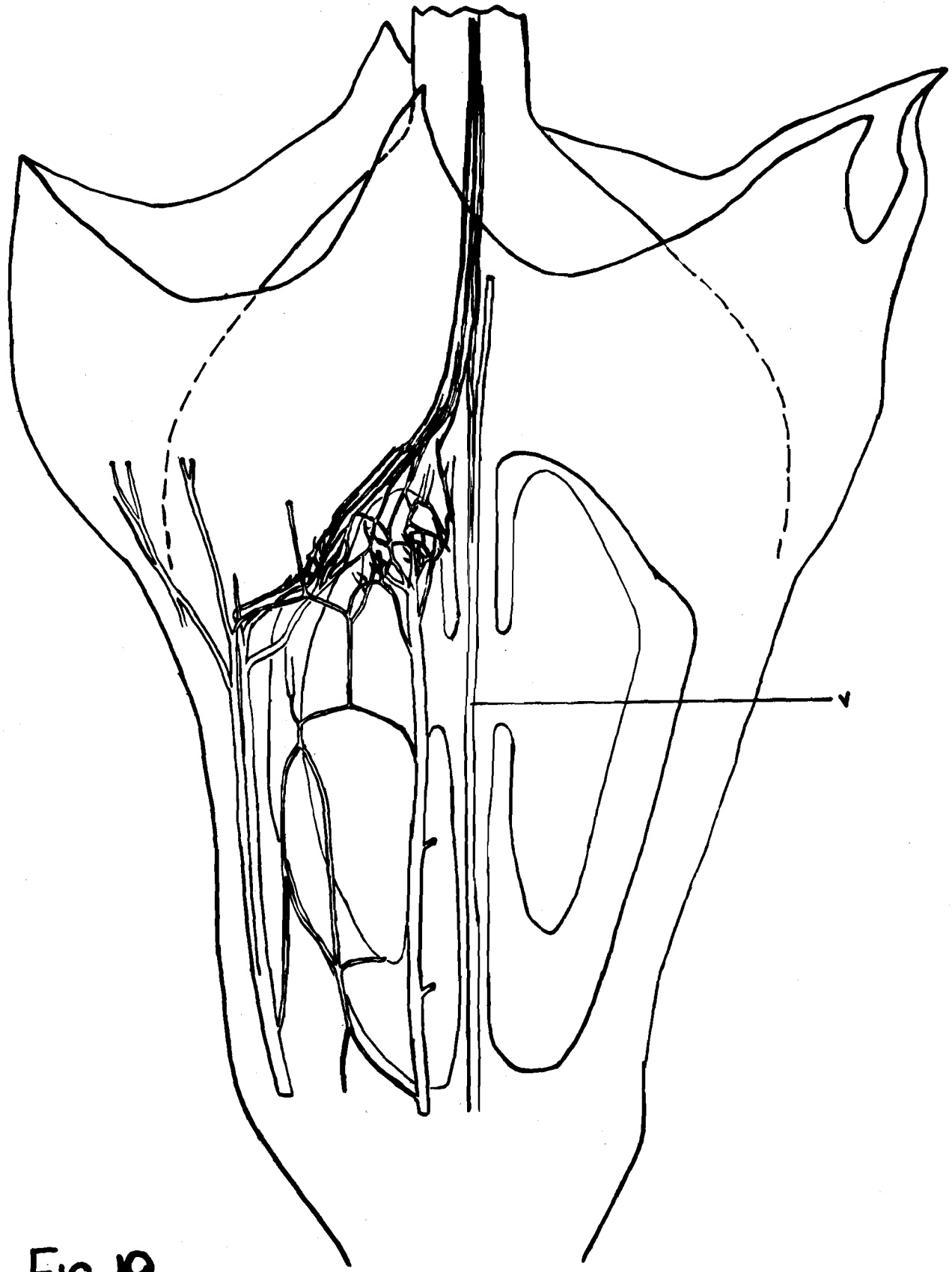


FIG 19

Fig. 20 Simplified schematic reconstruction of vascular system of Escallonia exoniensis.

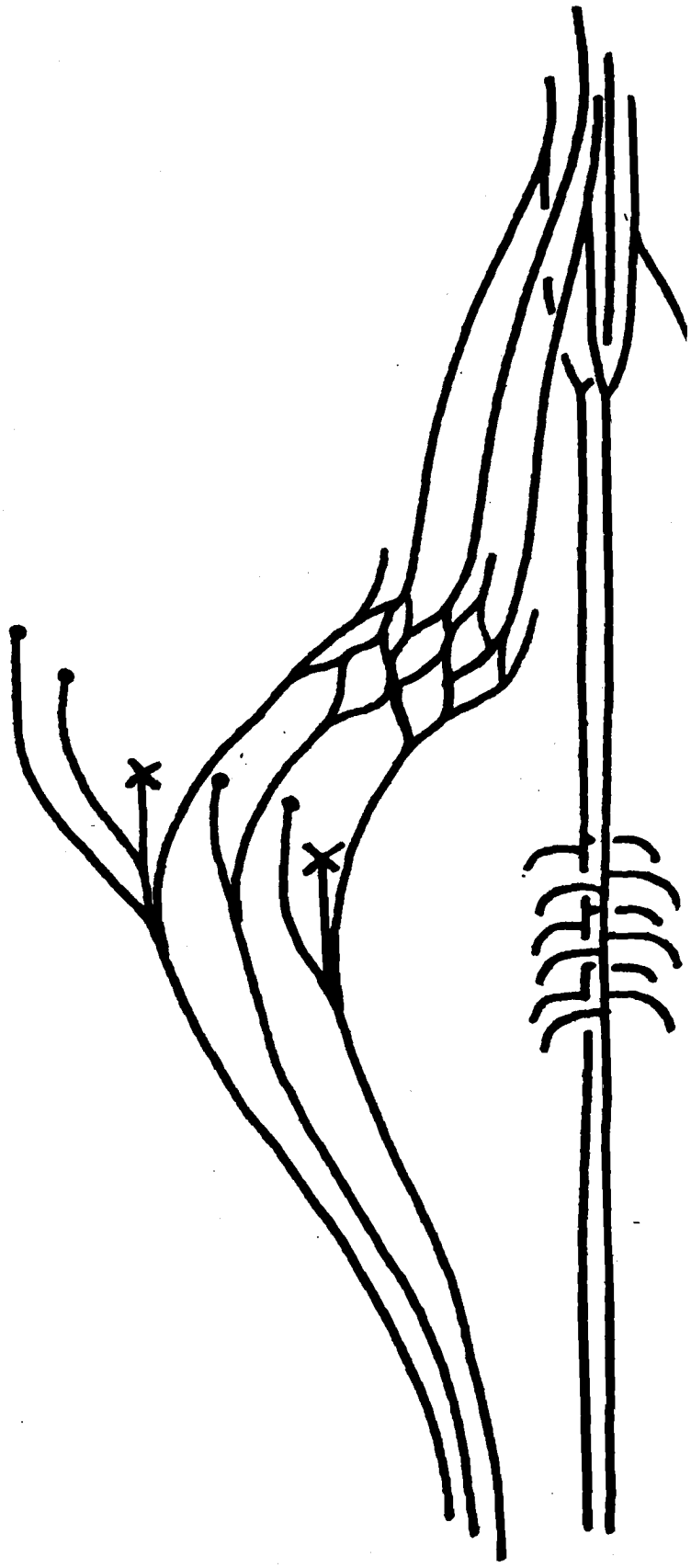


FIG. 20

carpels, the details of placentation, and the degree of cohesion of the whorls of floral organs. The vasculature of all can be described in the same general terms. In each there is an outer framework of bundles which supplies the three outer floral whorls. Two other systems supply the gynoecium. The first of these or dorsal system branches inwards from the outer framework, supplies the disc, and continues into the style. The second or ventral system runs axially up the centre of the gynoecium, provides the ovular branches, and continues upwards to meet the dorsal system in the style.
This common pattern is found not only in the three New Zealand genera but also underlies the vasculature of Escallonia itself. Perhaps the feature which characterizes them all most clearly is the presence of vascular bundles ending blindly in the disc. It may therefore be concluded that the floral morphology of the three genera is basically similar and that they conform to that characteristic of the family.

CHAPTER III.

WOOD ANATOMY

The vegetative shoots of the three genera bear exstipulate simple leaves with serrate margins. The phyllotaxis of *Carpodetus* and *Quintinia* is spiral, in *Ixerba* it is variable being either sub-opposite, sub-verticellate or spiral. The arrangement of the leaf traces in all the three genera is tri-lacunar (fig. 21). This agrees with the findings of Swamy (1954). This author found the nodal anatomy to be variable within the family most genera being uni-locunar. One species, *Argophyllum laxum*, is penta-lacunar.

The anatomy of the secondary xylem has been fully described for one of the genera, namely *Carpodetus* (Brook, 1950). The present investigation fully confirms this description which is reproduced here:

> "The secondary wood is almost white in colour, with obscure growth rings, but prominent rays along with it invariably splits as it dries. The wood is diffuse-porous, annual ring boundaries being defined by the contrast between summer and spring wood vessel diameters. Ray cells broaden tangentially in the summer wood. No tracheids are present, the vertical conducting cells all being vessels. By Chattaway's standards these vessels are very numerous, and their thin-walled, angular segments have a 'small' tangential diameter and are 'extremely long.' (For actual measurements see Table of Descriptions.) Segment end walls

Fig. 21. Transverse sections through the leaf node

(A) *Quintinia acutifolia*

(B) *Ixerba brexioides*

(C) *Carpodetus serratus*

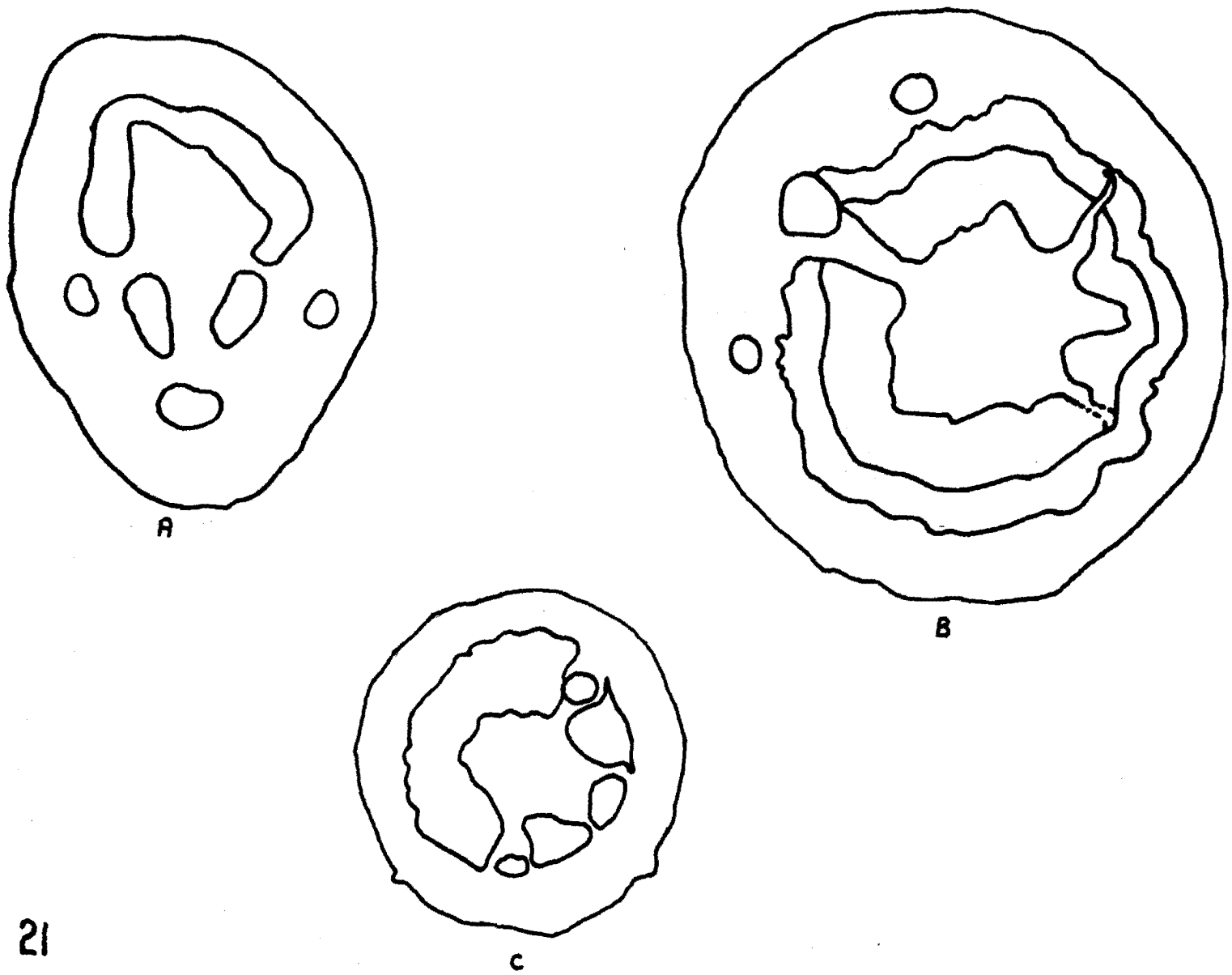


FIG 21

are very oblique, often with tails, and with numerous narrow, fully-bordered perforations which are always scalariform. The vessel pitting is opposite. Except for this last feature, which is considered slightly more advanced than scalariform pitting, the vessel segment is primitive in every respect. Very oblique end walls are the rule in woods such as Carpodetus which are not storied. The bulk of the tissue between the vessels is comprised of fibres, which by Chattaway's standards are 'very long' and 'thin' walled. Pitting is fairly evenly distributed, on all walls, the pit chambers easily visible, borders strongly developed, and the inner apertures narrow and included. Such fibres are classed as fibre-tracheids and considered to be a somewhat primitive type. As Priestley has established as generally true, pits are not formed between fibres and other elements. Vertical parenchyma are diffuse, the cells in similar vertical series to the phloem parenchyma. Ray structure conforms with Krib's heterogeneous type 1, which both he and Barghoorn consider the most primitive in Angiosperms. In this type the uniseriate rays are high and composed of vertically elongated cells. The multiseriate rays possess high uniseriate tips identical with the uniseriate rays, and are in their multiseriate parts parallel-sided with elongated lateral cells. Primary multiseriate rays are, of course, of interfascicular origin. Secondary ones were observed to arise by two of the methods described by Barghoorn - i.e., by widening of a uniseriate ray or by coalescence of several such rays, and they are occasionally split apparently by changeover from ray to fusiform initials in the cambium. On Chattaway's standards these rays are 'very broad' and 'extremely high.'

.....

Table of Description of Secondary Wood.

Stem Wood of Carpodetus serratus Forst.

Vessels:

(a) Measurements:

	Mean	Standard Deviation	S.D.of Means
Total Segment Length	1041.0μ	220.21μ	88.991μ
Radial Diameter	47.9μ	12.677μ	5.6909μ
Tangential Diameter	35.1μ	10.809μ	3.9089μ

(b) Number: Vessels more or less evenly distributed.

Range from 40-110, but mostly 50-80 pores or groups per square millimetre.

(c) Grouping: Vessels solitary or in groups of 2-4, about 60% solitary and about 35% in pairs.

Fibres:

Mean Fibre Length	=	1653.0μ
Standard Deviation	=	301.1μ
Standard Deviation of Means	=	166.2μ

Rays:

(a) Height: Multiseriate rays vary from 450μ-13200μ with about 60% from 1400μ-3000μ. Uniseriate rays vary evenly from 150μ-4150μ.

(b) Width: About 75% are uniseriate. The multiseriate rays vary from 2-16 cells in width, with about 55% from 5-8 cells, and about 15% 2 cells wide."

The only addition that can be made to this description is that the contrast between the spring and summer wood is due to the greater frequency of vessels in the former, as well as to their greater size.

The woods of Quintinia and Ixerba were found to be very similar to that of Carpodetus. (These similarities are shown to some extent in fig. 22 and in the photographs of the three woods, figs. 23, 24, 25 & 26, 27 & 28.) It is, therefore, unnecessary to set out each description in full. Instead the points of difference will be noted.

Quintinia. The vascular rays are of the same types as in Carpodetus but both the multiseriate and uniseriate rays are much shorter (compare measurements in Table with those of Brook) and the multiseriate rays

Fig. 22. Drawings of vessels

(A) Quintinia acutifolia
(length 1273μ diameter 35μ)

(B) Ixerba brexioides
(length 1117μ diameter 55μ)

(C) Escallonia exoniensis
(length 445μ diameter 47μ)

FIG 22

Fig. 23. Photomicrograph of wood of Carpodetus serratus transverse section.

Fig. 24. Photomicrograph of wood of Carpodetus serratus tangential longitudinal section.

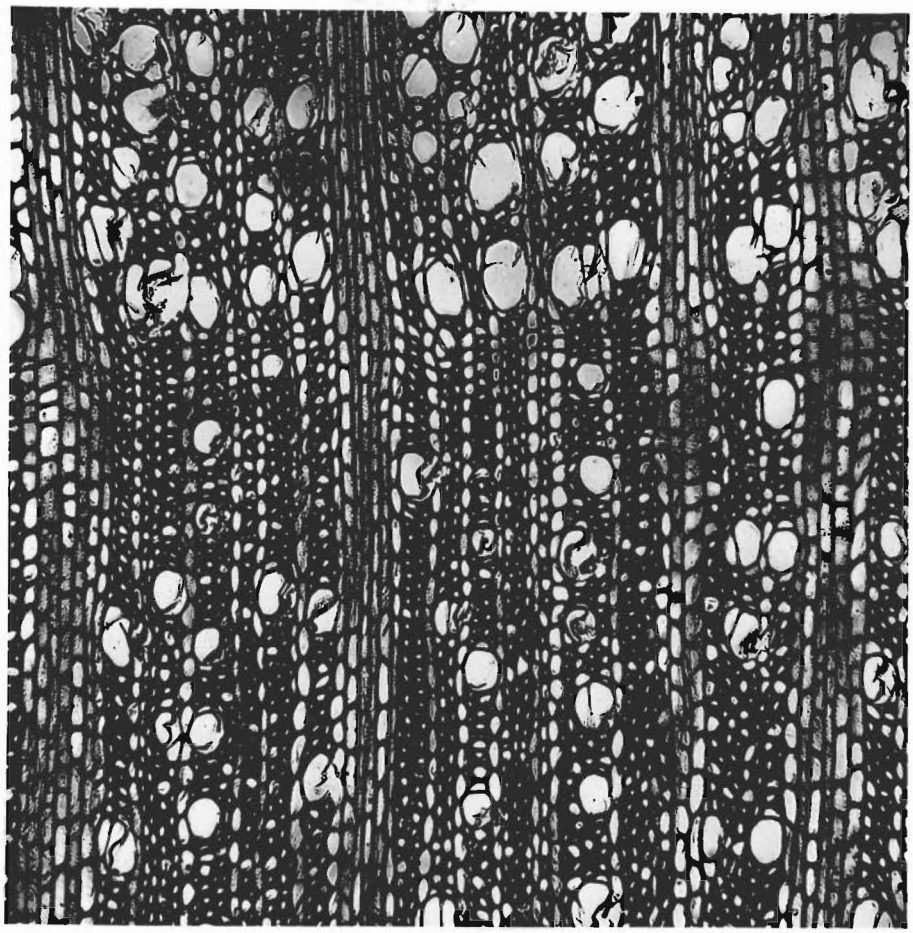


Fig. 25. Photomicrograph of wood of Ixerba brexioides transverse section

Fig. 26. Photomicrograph of wood of Ixerba brexioides tangential longitudinal section

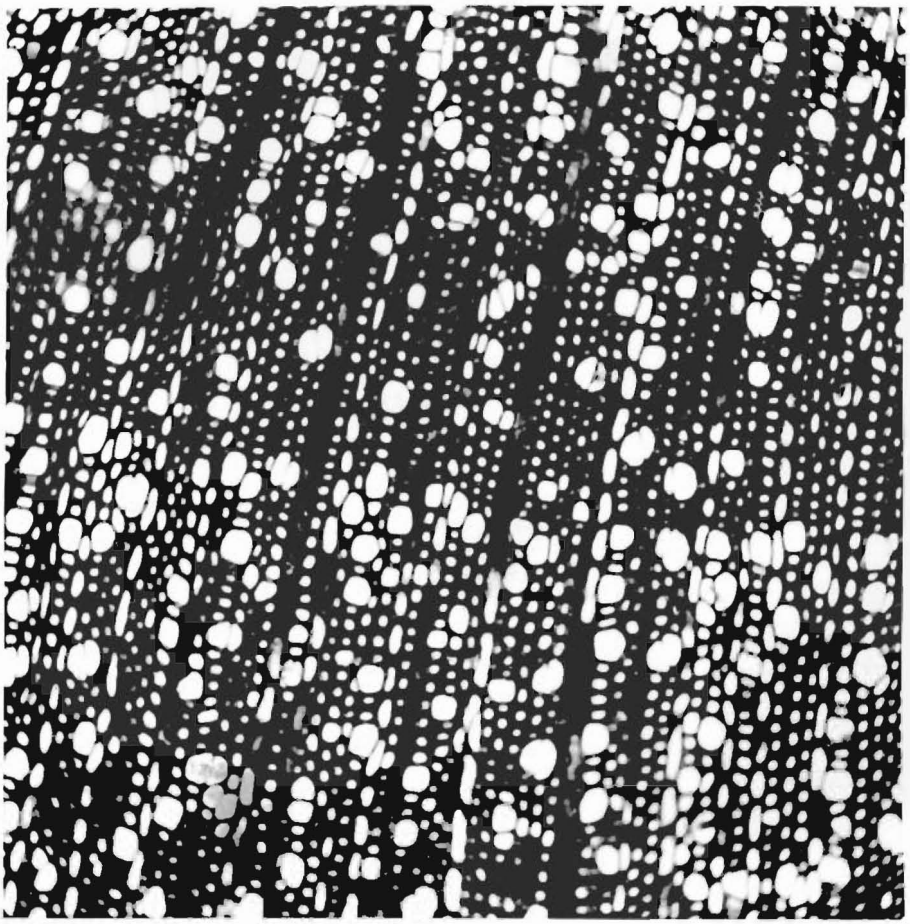
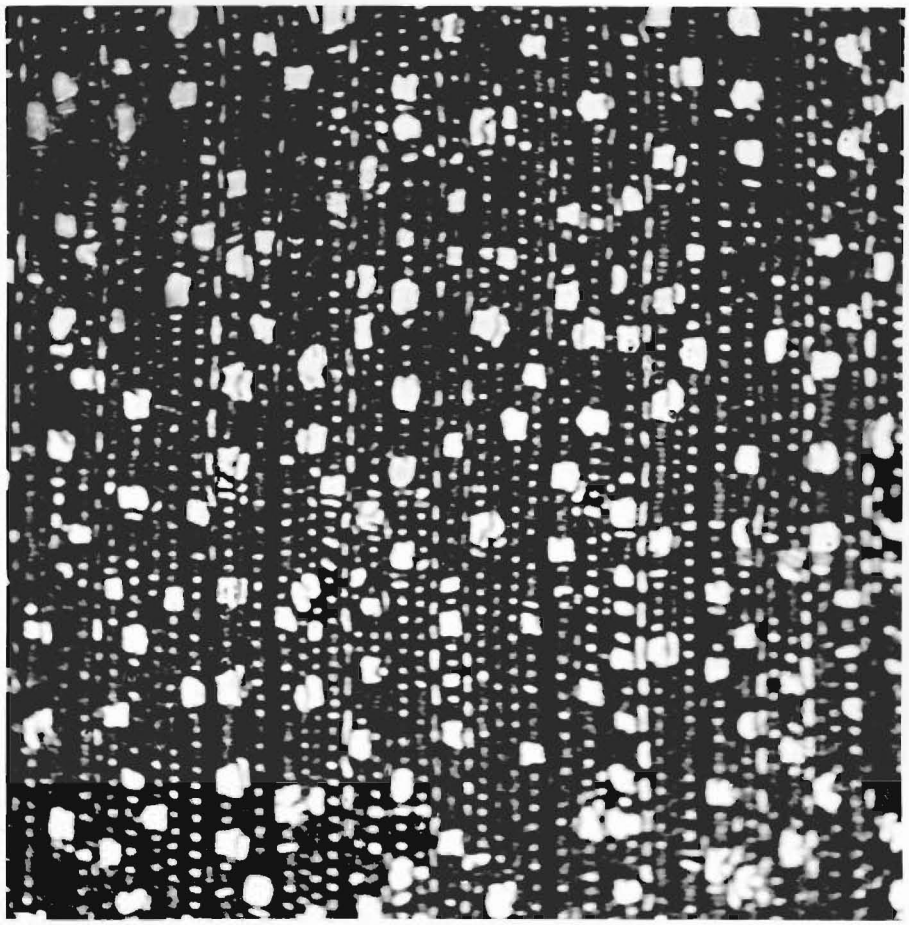
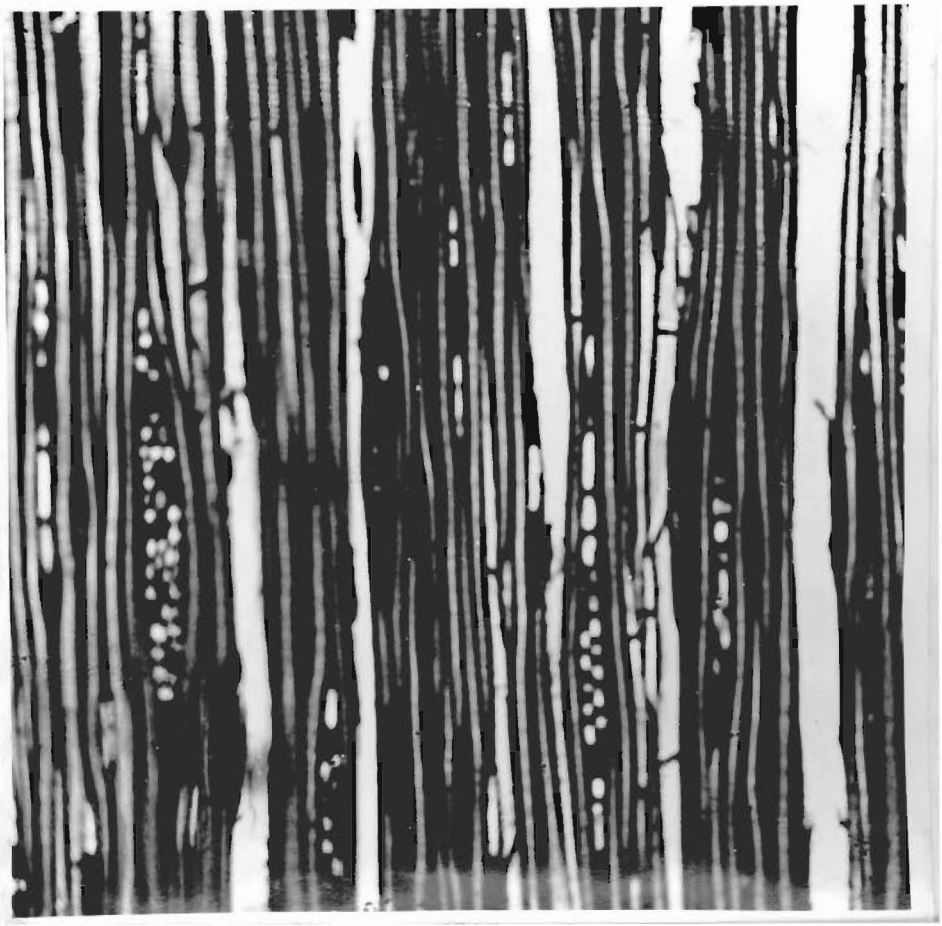


Fig. 27. Photomicrograph of wood of Quintinia acutifolia transverse section.

Fig. 28. Photomicrograph of wood of Quintinia acutifolia tangential longitudinal section.





are much thinner (most are less than five cells wide while the majority of those of Carpodetus are between five and eight cells wide). The lateral cells of the multiseriate rays are not vertically elongated and the rays lack the high uniseriate tips that are typical of the multiseriate rays of Carpodetus. In addition the lumen of the vessels is smaller and the fibres are more rectangular in outline. The distinction between spring and summer wood is less clear.

Ixerba. The wood is very similar to that of Carpodetus in the distribution of vessels, distribution of spring and summer wood, size of vessels and shape of fibres. The rays, however, show some differences. The multiseriate rays, which occur much less frequently than do multiseriate rays in Carpodetus, are extremely thin, (usually only two or three cells wide). They consist of a short multiseriate portion on each side of which is a long uniseriate tip. The numerous uniseriate rays resemble those of Quintinia although they tend to be somewhat longer. (See Table of Measurements).

Escallonia. For the purposes of comparison one sample of the wood of Escallonia exoniensis was also examined. This was seen to closely resemble the wood of Carpodetus and the wood of the other two genera. One difference that was noted was that the vessel elements and fibres

tend to be markedly shorter than those of the other three genera. Also it was noted that the prominent multiseriate rays are shorter and thinner than those of Carpodetus although wider than those of Quintinia and Ixerba. Similar to Carpodetus these rays have uniseriate tips but these are much shorter than they are in Carpodetus. The uniseriate rays are relatively uncommon.

Although a limited number of specimens was examined and these from trees of varying age, dimensions of fibres, vessels and rays are given. These will not indicate the full range of dimensions present in any species but are presented for comparison with the measurements of Carpodetus produced by Brook.

Table of Measurements of Woods of Ixerba, Quintinia and Escallonia.

25 measurements per sample.

Ixerba.

Vessel length	Range	Mean	Standard Deviation
Sample 1	523μ-1578μ	1188 μ	191.5μ
Sample 2	720μ-1400μ	998 μ	179.2μ
Sample 3	742μ-1540μ	1203μ	248.4μ
Sample 4	578μ-1242μ	867μ	181.3μ
Tangential vessel diameter.			
Sample 1	17μ-44μ	29 μ	7.35μ
Sample 2	19μ-49μ	33μ	7.18μ

	RANGE	MEAN	STANDARD DEVIATION
Sample 3	14μ-36μ	25μ	5.62μ
Sample 4	18μ-42μ	27μ	6.12μ

Fibre length.

Sample 1	703μ-1938μ	1281μ	272.3μ
Sample 2	836μ-1547μ	1297μ	190.9μ
Sample 3	641μ-1977μ	1297μ	234.8μ
Sample 4	828μ-1594μ	1117μ	182.8μ

Ray size.

Multiseriate

	Length		Width	
	Range	Mean	Range	Mean
Sample 1	180μ-930μ	539μ	20μ-39μ	25μ
Sample 2	33μ-1625μ	757μ	23μ-39μ	31μ
Sample 3	328μ-1422μ	703μ	20μ-51μ	29μ
Sample 4	391μ-1727μ	804μ	20μ-31μ	26μ

Uniseriate

	Length		Width	
	Range	Mean	Range	Mean
Sample 1	78μ-930μ	421μ	12μ-27μ	18μ
Sample 2	141μ-969μ	429μ	12μ-23μ	18μ
Sample 3	141μ-1484μ	578μ	12μ-23μ	15μ
Sample 4	164μ-1289μ	570μ	12μ-23μ	16μ

Quintinia

Vessel length	Range	Mean	Standard Deviation
Sample 1	1055μ-1773μ	1438μ	212.4μ
Sample 2	469μ-1336μ	891μ	220.2μ
Sample 3	633μ-1555μ	1164μ	265.6μ
Sample 4	828μ-1422μ	1180μ	188.8μ

Tangential vessel diameter.

Sample 1	16μ-39μ	24μ	6.68μ
Sample 2	20μ-39μ	34μ	5.57μ
Sample 3	20μ-47μ	34μ	7.35μ
Sample 4	16μ-39μ	29μ	6.6μ

Fibre length.

Sample 1	1188μ-2064μ	1563μ	236.5μ
Sample 2	586μ-1523μ	1156μ	247.6μ
Sample 3	898μ-1555μ	1266μ	179.1μ
Sample 4	883μ-1961μ	1273μ	257.3μ

Ray sizes.

Multiseriate

	Length		Width	
	Range	Mean	Range	Mean
Sample 1	281μ-1016μ	570μ	16μ-55μ	30μ
Sample 2	281μ-1000μ	523μ	23μ-55μ	34μ
Sample 3	242μ-1422μ	602μ	27μ-59μ	38μ
Sample 4	328μ-1884μ	656μ	23μ-43μ	32μ

Uniseriate

	Length		Width	
	Range	Mean	Range	Mean
Sample 1	121μ-664μ	328μ	8μ-16μ	13μ
Sample 2	86μ-883μ	375μ	16μ-23μ	19μ
Sample 3	102μ-719μ	383μ	12μ-23μ	19μ
Sample 4	188μ-1796μ	609μ	12μ-27μ	17μ

Escallonia	Range	Mean	Standard Deviation
Vessel Length	375μ-665μ	531μ	68.2μ
" diameter	20μ-39μ	31μ	6.67μ
Fibre length	578μ-1141μ	828μ	134.8μ

Ray sizes.

Multiseriate

Length		Width	
Range	Mean	Range	Mean
203μ-1250μ	523μ	16μ-43μ	25μ

Uniseriate

Length		Width	
Range	Mean	Range	Mean
148μ-961μ	406μ	12μ-20μ	14μ

An inspection of the above dimensions confirms the conclusions reached after a comparison of the anatomical structure of the wood; that is to say, the dimensions of vessels and fibres are similar in the three New Zealand genera. The "extremely long" (Chattaway 1932)

vessel elements with "very small" diameters support the view that these three genera are related. Metcalfe & Chalk (1950) publish graphs showing the frequency among Dicotyledonous woods of vessel-element lengths and diameters. Reference to these graphs shows that both the great length and small diameter of these vessel elements fall into infrequent size ranges. This supportsthe conclusion that the nature of the vessel element is highly characteristic. The vessel elements of Escallonia are considerably shorter (fig. 22) (though "long" by Chattaway's definitions). This character however, does not appear sufficient, in the face of so many other characters of the woods which are similar, to warrant the conclusion that Escallonia is unrelated to the New Zealand genera under consideration.

A feature of the wood of Ixerba and Quintinia is the similarity in length between the fibres and the vessel elements. As it is typical for the fibres of Dicotyledonous woods to be considerably longer than the vessel elements (see Bailey 1920), the fact that these woods are alike in this second unusual feature is good evidence in support of the view that they are related.

A comparison of the proportions of wood elements, and in particular the ratio of breadth to length

of the vessel elements and of the height to width of rays is likely to be particularly helpful. These are set out in the table below.

	Ratio length/breadth vessels	Ratio height/width multiseriate rays
Carpodetus	29.66	Not available
Ixerba	37.3	25.3
Quintinia	38.5	17.5
Escallonia	17.1	20.9

The ratios for the vessel elements agree well for Quintinia and Ixerba and that for Carpodetus is similar. As would be expected, the ratio for Escallonia is less, but is comparatively large, confirming the extremely narrow type of vessel present. The ratio shown by the rays confirms that they are similar in shape in the species, though those of Quintinia are relatively broader. (As no measurements of the widths of the rays of Carpodetus were available ratios could not be worked out for this species.) As noted previously the multiseriate rays of Carpodetus are often very high and wide, but their shape is similar to that of the other genera. Other genera of the Escalloniaceae from Australia possess rays as large as those of Carpodetus, which are, therefore, within the range of variation known within the family.

SUMMARY OF CONCLUSIONS

The purpose of the investigations reported in this thesis was to test the possibility that one or all of the three genera, Carpodetus, Ixerba and Quintinia might not be correctly placed in the Escalloniaceae. Differences in floral structure and in the characters of the vegetative shoots suggested that the three genera might not all be related to one another. The most striking feature of the flowers of the three genera is the varying relationship between the outer floral appendages and the gynoecium. An equally striking difference, but in the vegetative organs, is the arrangement of leaves on the stem. These are clearly spiral in Carpodetus and Quintinia but are usually described as opposite in Ixerba. They certainly often appear to be strictly opposite, but at other times appear merely as a condensed spiral and successive leaves may even be separated by considerable internodes.

Two lines of evidence were examined in the hope that new facts from two unrelated systems of the plants would determine the relatedness or distinctiveness of these genera.

As has been recorded above, the vasculature of the flowers of all genera appear to be referable to a common overall plan. This plan is modified according to the relative position of the perianth and ovary and according to the number of members in successive whorls, but it remains constant in its essential features. These are a system of strong bundles supplying the two perianth whorls and the stamens: from this arises the bundles of the carpel walls which continue into the styles. The ventral bundles are axial and also continue into the styles. A similar system was also found in the type genus of the family, Escallonia. It is true that such a pattern of bundles is very simple and of itself might not indicate relationship; it merely does not contradict the possibility. However, there is at least one feature of the vasculature of these flowers which is more characteristic. The disc which is developed around the gynoecium (at its apex or lower down, according to the architecture of the flower is copiously supplied by small or even strong bundles. These may be branches from any or all of the principle bundles (i.e. stamen, petal and sepal traces as well as the dorsals). They may end blindly or may join to form a complex network as in Escallonia and Ixerba. From this network around the base of the style the supply of the styles may arise,

in which case it may not be possible to trace the direct connection of the dorsal bundles with those of the style. This well developed vascular supply to the disc appears to form a more positive link between all these genera. For this reason it is felt that this line of evidence can be considered to afford information that the three genera are correctly placed in the same family as Escallonia.

The evidence afforded by wood anatomy is rather similar in that the resemblances are mostly of a very general nature. Nevertheless their association together at least suggests affinity and one other feature which they share is more unusual and provides more positive evidence of relationship.

The characters shared by these woods are numerous but of a generalized nature. They can be summarized as a diffuse arrangement of vessels made up of elements of a very primitive type. These are embedded in copious background of angular fibres with bordered pits (fibre - tracheids). The rays are heterogeneous. The size of multiseriate rays in the Escalloniaceae is variable (Tippo, 1938 and unpublished information from Professor Philipson). The rays of Carpodetus are considerably larger than those of the other genera (Eyde 1966), but as was shown above, their shape is not dissimilar. The three genera therefore

fall within the range of variation found within the family.

The most striking feature of Ixerba and Quintinia and to a lesser degree Carpodetus and Escallonia is the extreme length and narrowness of the vessel members which approximate to that of the fibres in the first two genera. It is this character that appears to suggest that the similarity of their wood anatomy is due to relationship rather than the chance association of generalized and primitive characters. It is therefore concluded that both lines of evidence investigated point in the same direction, namely, that the three genera Carpodetus, Ixerba and Quintinia are related to one another and are correctly placed in the Escalloniaceae.

ACKNOWLEDGEMENTS

It is with grateful thanks that the author acknowledges his great debt to Professor W. Philipson for his assistance throughout the preparation of this thesis.

Thanks are also due to

Mr. A. McAusland of the Botany Department for help in preparation of material.

Mr. F. McGregor of the Botany Department for his work in presenting the drawings and photographs in their final form.

Mr. M. Jellie, Mr. P. Joyce, Mr. R. Shea and N.Z. Forest Service, Rotorua for help in obtaining material.

Mrs. G. Smith for assistance with the typing.

My wife for her constant encouragement.

BIBLIOGRAPHY.

ALLEN, H.H. (1961), Flora of New Zealand, Vol. 1, Wellington

BAILEY, I.W. (1920) The Cambium and its Derivative Tissues II Size Variations of Cambium Initials in Gymnosperms and Angiosperms. Amer. J. Bot. 7:355-367

BENTHAM, G. & HOOKER, J.D. (1867) Genera Plantarum Vol. 1 (3). London

BROOK, P.J. (1950) Vegetative Anatomy of Carpodetus serratus Forst. Trans. Roy. Soc. N.Z. 79:276 - 285

CHATTAWAY, M.M. (1932) Proposed Standards for Numerical Values used in Describing Woods. Tropical Woods 29:20-28.

ENGLER, A. (1930) Saxifragaceae, in Engler, A. and Prantl, K. Nat. Pflanzenfam. Aufl. 2. 18 (a). pp. 74-226.

EYDE, R.H. (1966) Systematic Anatomy of the Flower and Fruit of Corokia. Amer. J. Bot. 53:833-847

HUTCHINSON, J. (1926) The Families of Flowering Plants 1st Edn. Oxford

HUTCHINSON, J. (1959) The Families of Flowering Plants 2nd Edn. 2 Vols. Oxford

SWAMY, B.G.L. (1954) Morpho-taxonomical Notes on the Escalloniaceae, Part A. Nodal and Petiolar Vasculature. J. Madras. Univ. B. 24:299-306.

TIPPO, O. (1938) Comparative Anatomy Moraceae and Their Presumed Allies. Bot. Gaz. 100: 1-99.